THE BOTANICAL GAZETTE

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THE BOTANICAL GAZETTE

EDITOR

JOHN MERLE COULTER

VOLUME LII

JULY–DECEMBER, 1911

WITH TEN PLATES AND ONE HUNDRED AND THIRTY FIGURES

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ERRATA

P. 24, line 3 from bottom, omit *Cornus canadensis*.
P. 24, line 1 from bottom, for *Prunus* read *Pyrus*.
P. 26, line 7 from bottom, omit *Alnus incana*.
P. 27, line 7 from top, for *ovata* read *canadensis*.
P. 210, line 18 from top, for spongioplasm read cytoplasm.
P. 237, footnote 1, for Ernest read Ernst.
P. 264, line 18 from top, for *Roripa terristris* read *Roripa terrestris*.
P. 273, line 5 from bottom, for anthers dehiscent read anthers dehiscent to but not through the apex.
P. 330, line 26, for formula read formulae.
P. 395, fig. 3 legend, for gasket read socket.

Vol. LII No. 1

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July 1911

Editor: JOHN M. COULTER

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Issued July 17, 1911

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THE

BOTANICAL GAZETTE

JULY 1911

THE VEGETATION OF CRANBERRY ISLAND (OHIO) AND ITS RELATIONS TO THE SUBSTRATUM, TEMPERATURE, AND EVAPORATION.[1] I

ALFRED DACHNOWSKI

(WITH SEVEN FIGURES)

The object of the present paper is to give, as briefly as is consistent with a limited presentation, the major conditions of some of the factors which have been found limiting the activity of plants in bogs.

The striking discontinuity of bogs in distribution, the absence of genetic relationship between bog plants and the surrounding flora of states in the latitude of Ohio, and the floristic agreement of these plants with the vegetation of the distant north has invited the attention of many students of ecology.

As early as 1872 a solution of this interesting problem had been formulated by GRAY (**14**) in his glacial relict theory. A similar explanation has been advanced by numerous recent writers, and the broader relations which involve comparative studies have been well established (**31**). However, the reciprocal relations of these plants and their habitat, the demands which the plants make on their environment, the means which they employ, and the functional rôle which the particular species perform; in short, an investigation of factors by which the present associations are determined and which would account for the existence and the peculiarities, structural and functional, of these "boreal" plants

[1] Contribution from the Botanical Laboratory, Ohio State University, no. 61.

on the basis of their relation to the present ecological conditions of their habitat, this has been a far more difficult matter and has not met with unanimity of opinion. A knowledge of the flora of a region and the floristic status of successive periods of time is indispensable, if for no other reason than to indicate the various conditions frequented by species or groups of plants. But the statistical method must be supplemented by an adequate study of experimental tests. The varying activity of plants as individuals and communities is of greatest importance scientifically and must be determined in the field under measured conditions.

Various theories have been put forward from time to time as to the environmental relations of plants in bogs, but none of them can be said to have brought nearer a solution of this phase of the problem. The historical aspect of the question need not be dealt with here in detail. The more important theories are those advanced by the following writers: KIHLMAN (**19**) regards low temperature and strong drying winds as the prominent factors in high northern latitudes; SCHIMPER (**29**) emphasizes humus acids in the soil, abundance of soluble salts and alkalies, and regards bog habitats as being "physiologically dry"; LIVINGSTON (**22**) suggests the presence of chemical substances not in direct relation to acidity of the soil as acting on the vegetation; WARMING (**32**) is inclined to look upon the presence of free humus acids as the weightiest cause; FRÜH and SCHRÖTER (**13**) correlate the conditions with low temperature and lack of aeration in the soil; while SCHWENDENER (**30**) and CLEMENTS (**5**) hold that the structural peculiarities are not at all related to present habitat conditions but are primitive peculiarities, which now remain unaltered but were originally developed under different xerophytic conditions. Another explanation, that of the toxicity of the habitat, and its consequent physiological aridity and selective operation upon forms striving for occupancy, has been offered by the writer of this paper. This view has come from a more detailed investigation of the physical and chemical characteristics of bog soils and their physiological property (**7, 8**). It emphasizes the active participation of specific microorganisms and fungi, a view which correlates also very well with the unproductiveness of differ-

ent peat soils under cultivation examined by the writer, and lays stress not alone upon structural characteristics in plants but also upon limiting habitat conditions as conducive to the development of place-functions. That various factors enter into the problem, and possibly many others not yet discovered have a part directly or indirectly, is clearly recognized.

Further field work on the bog plant societies has been carried out especially with a view to test the reference made by several writers to the part played by low substratum temperature and by the evaporating power of the air. In addition, studies on the physical, chemical, and biological problems of the substratum were continued.

It is obvious that the physical conditions, whether temperature or evaporation, if sufficiently great in their differences, must have an important bearing on the question of distribution and of xerophytism in bog plants. The larger part of the body of bog plants is imbedded in the peat at various depths. The various functions take place only within lower and upper critical conditioning factors. For instance, the germination of seeds, the activity of roots and rhizomes, the permeability of protoplasmic membranes, the rate of absorption and chemical action during growth in underground organs, must be greatly affected by the actual extreme temperatures encountered, as well as by the rapidity with which changes in temperature occur. The diurnal and seasonal temperature changes in the peat soil, and the differences in temperature between the aerial and underground portions of plants cannot fail to be of equally great importance in the physical and chemical processes, in the activity of the soil organisms on those biological changes which modify soil productiveness, and in the reciprocal physiological influences upon which absorption, transpiration, and transport of solutions from one part of the plant to another depend. The task of securing a coordination between these functions must be indeed a complicated one, varying greatly in different species according to their capacity of endurance. It is therefore clear that conditions as regards efficient temperature determine greatly the physiognomy of the individual plant and of the whole of the vegetation in habit of growth and distribution. But the rôle

which temperature plays quantitatively and qualitatively in the distribution of bog plant societies is in the main not known. So far as the writer is aware, no quantitative measurements between temperature as a probable causative or limiting factor and the resulting function and form in bog plants has been previously conducted, such as would afford any definite record of the actual physical conditions obtaining at different substratum levels in a bog vegetation. What has been said for temperature holds true also for evaporation. The influence of this and other factors is among the pressing problems of physiological ecology. From this point of view the data presented below have been collected in the field during the past three years.

The physical factors which modify and more or less control the community of plants on Cranberry Island have been formulated for the most part quantitatively. Yet it must be frankly admitted that, at the present time, interpretation of the data thus far gained is still only in part possible. Though the data have been gained laboriously through many months, and to the writer seem convincing, to attempt to correlate these accurately may be ill-advised. Only by the multiplication of such data will it be possible to express the results with quantitative exactness. The very necessity, however, of recording and accumulating an extended series of comparative observations is the justification of publishing now the data at hand. The conclusions here expressed, therefore, are still tentative, and true for the local investigation only.

Frequently the writer's students have assisted in this work, and acknowledgment is due to Messrs. L. W. SHERMAN, E. WRIGHT, E. LINN, L. KING, and M. G. DICKEY for efficient aid. The warmest thanks of the writer are expressed here also to Professor J. R. CHAMBERLAIN, who surveyed the island, to Professors N. W. LORD, W. E. HENDERSON, and C. W. FOULK for cooperation in the chemical analyses, and to Miss F. DETMERS for identification of plants and the care with which the floristic study has been generally furthered. The expense of the field work has been covered in large part by a special grant from the Emerson McMillin Research fund.

The habitat

The field work which forms the basis of the present paper was carried on at Buckeye Lake, Ohio. The geological record of the region is for interest second to few places in Ohio. The strata furnish an almost unbroken narrative from the Silurian up to the Tertiary. It is a rare thing to find peat bogs in Ohio south of latitude 40°, and this circumstance makes the locality as the southernmost limit of existing peat formations still more interest-

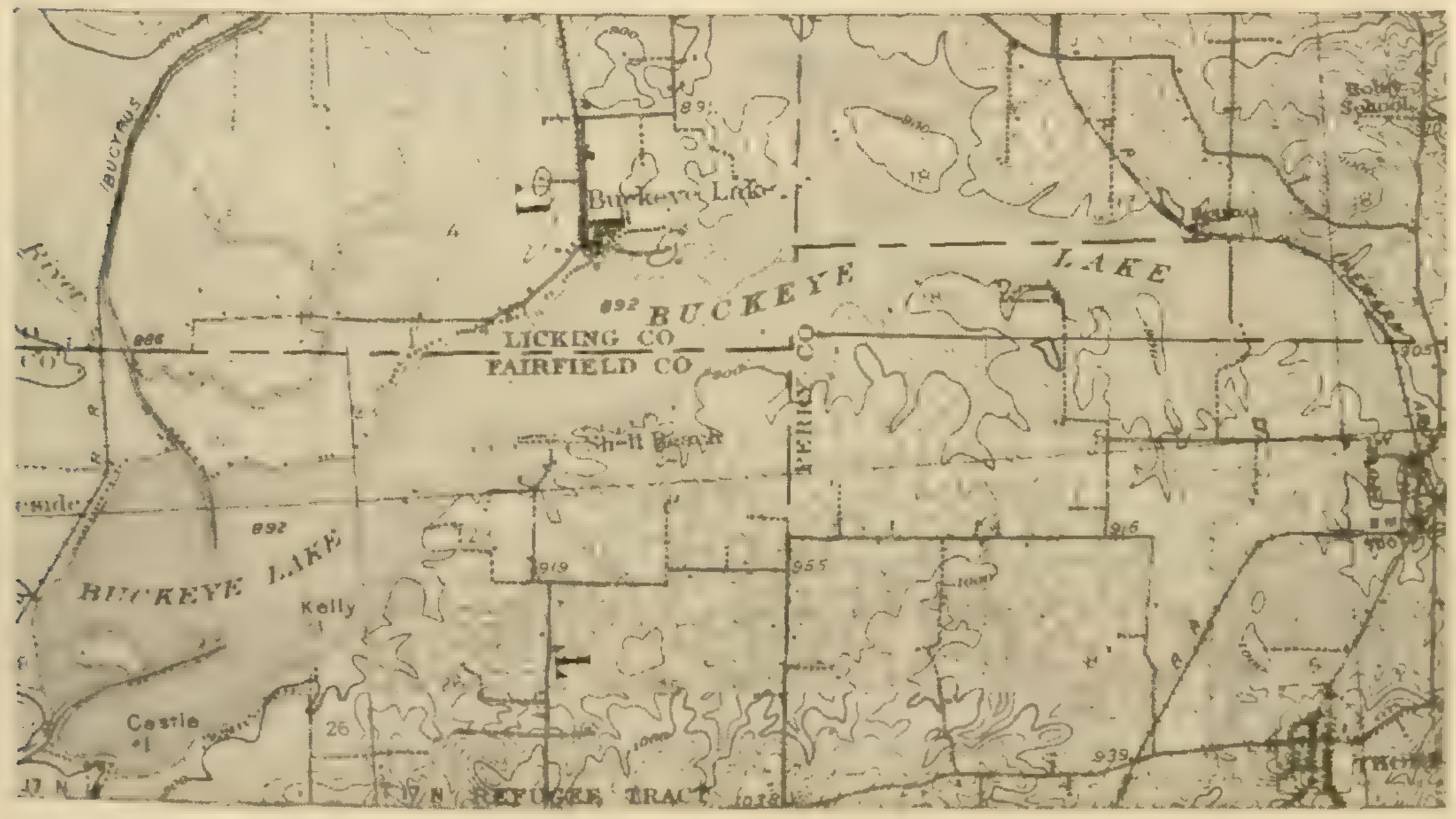

FIG. 1.—Topographic map of Buckeye Lake and vicinity; U.S. Geological Survey, 1907; contour interval 20 feet (6 m.); scale, 1 inch = 1 mile (2.5 cm. = 1.6 km.).

ing. And to complete the panorama of the great past, the remains of the moundbuilders found near Newark, Jacksonville, and other places in the vicinity continue the record down to the historical period.

Buckeye Lake is situated in Licking, Fairfield, and Perry counties, about 26 miles (41 km.) east of Columbus, and is at an elevation of 150 feet (45 m.) above that of the University campus. The area and location are shown on the Thornville sheet of the U.S. Geological Survey (fig. 1). The lake, like many others, is one characteristic of the highlands of watersheds throughout Ohio and adjoining states. The heath bogs in Wyandot County, the extensive bogs in Huron County, possibly among the largest

peat deposits in the United States, the Pymatuning tamarack swamp in Ashtabula County are similar members of this interesting chain of water basins marking the less perfectly drained summit of divides. The depressions on such summits receive water which creates no surplus and hence has almost no eroding powers. Buckeye Lake is now an extensive body of water, about 10 miles (16 km.) long, and one mile (1.6 km.) wide, but was originally a pond in the glacial drift, containing approximately 595 acres (238 hectars). Its chief water supply today is the south branch of the Licking River.

The lake basin lies near the southeastern margin of the terminal moraine. The main western member of the morainic system is about 3–5 miles (5–8 km.) in width. It presents marked differences in topography, the closely aggregated knolls and ridges rendering the belt readily distinguishable from the bordering plain. The knolls are generally conical in form with gentle slopes, ordinarily about 25–100 feet (7.5–30 m.) in height. These knolls were apparently formed at the time the gravel plain was being built up. They are thought to indicate that the head of the gravel plain was built up as a submarginal deposit to about its present height before the ice sheet had withdrawn from over it (**20**). The lake basin under discussion resulted from the comparatively slow retreat of glaciers and the consequent greater deposition of glacial material about the edge of a body of ice in an old glacial drainage channel. The "kettle" is characterized by comparatively steep slopes. Up to 1832 the lake was surrounded by about 3000 acres (1200 hectars) of swamp land covered with large trees (fig. 2). The report of Captain CHITTENDEN, as quoted by GRAY (**15**), gives the area of the lake at that time as 3300 acres (1320 hectars), which agrees very closely with its area as determined by later surveys. The present lake was formed in 1828 and completed in 1832, to serve as a reservoir for the Ohio and Erie Canal. The surface water was raised about 8 feet (2.4 m.) by forming a dike around the west end and a part of the north side of the swamp. It was hoped to supply the Ohio Canal with water from Newark to Little Walnut Creek, south of Lockville, a distance of 31 miles (5 km.), and the deficiency between Little

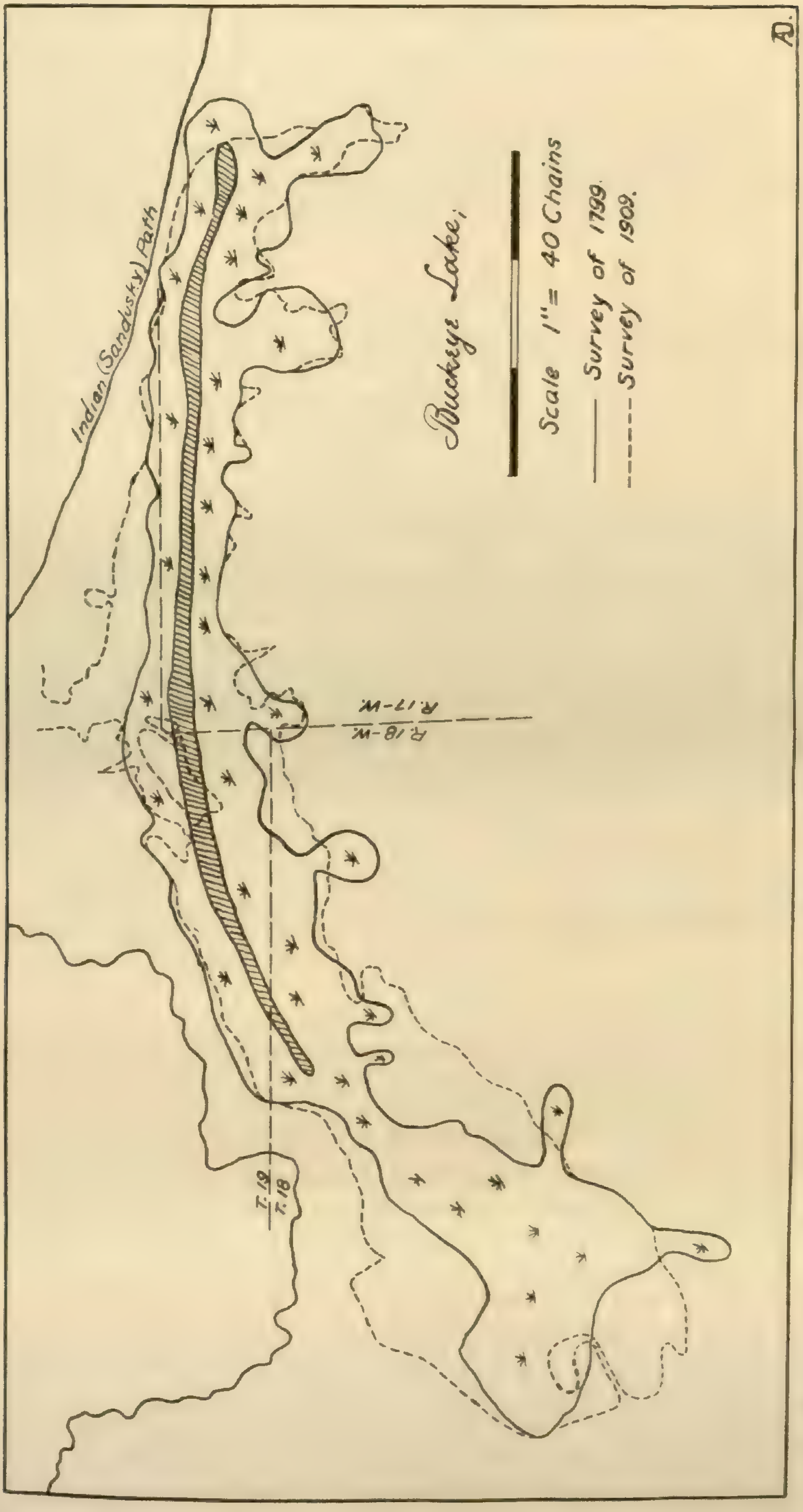

FIG. 2.—Buckeye Lake in 1799 and 1909; from tracings of the survey maps in the State Auditor's office at Columbus, Ohio.

Walnut Creek and Lockbourne. The reservoir soon proved inadequate for the canal, and in 1834 about 700 acres (280 hectars) were added, forming its present area. Its watershed embraces about 90 square miles (2331 hectars), which cannot be greatly enlarged. The lake then known as Licking Reservoir has, however, never stored a sufficient water supply and is not used for transportation purposes now. A large number of trees then standing soon died and fell into the water, where they remained beneath the surface. The majority of the trees were gradually cut away with

FIG. 3.—Cranberry Island; the view is from a hill northwest of the island near Buckeye Lake Station; to the left the woodlot; in the distance members of the terminal moraine; photographed August 1910.

their stumps exposed during low water. Only recently (the winter of 1908) the greater part of these stumps has been removed.

Near the northern bank of the lake, about one-half mile (0.16 km.) southeast of Buckeye Lake station, is the bog island, approximately one-tenth the dimensions of the lake (fig. 3). In position it is more or less sheltered by hills and a woodlot. The peat mass rises and falls with the changing water level of the lake, and supports a vigorous growth of trees, low bushes, sphagnum mosses, and cranberrries. Borings were made at various points on the island with a sampling tool devised by DAVIS (**2**), to determine the depth and the character of the peat. About 50 soundings were made, which indicate an average depth of peat of 30–35 feet (9–10 m.) along the southern shore of the bog island, and 11 feet

(3 m.) of peat along its northern shore. Borings made to the depth of 40 feet (12 m.) at the southernmost points of the island, and in the lake south of it, failed to reach bottom. The following table (I) gives some of the borings and related observations. The borings were made at a time when, for purpose of repair, the water surface of the lake was lowered 5 feet (1.5 m.) below the normal niveau.

TABLE I

ANALYSIS OF PEAT SPECIMENS FROM CRANBERRY ISLAND, BUCKEYE LAKE, OHIO

Analysis nos.	Station	Depth ft.	Depth meters	Description of peat samples
5.....	Central zone; sphagnum-cranberry	5	1.5	Brown, fibrous peat; mostly cranberry, sphagnum, and sedges.
7.....		14	4.2	Brown, non-fibrous, plastic peat with diatoms and shell marl.
8.....		25	7.5	Dark brown, well decayed, finely granular peat; algae (?) and filling from marginal borders.
9.....		40	12.0	Nearly black, non-fibrous, clayey peat.
11.....	Maple-alder zone	6	1.8	Dark brown, slightly fibered peat, coarser fibered below.
12.....		10	3.0	Brown and fibrous peat.
14.....		18	5.4	Dark brown, well decayed, finely granular peat with shell marl.
21.....		31	9.3	Fine sand with clay underneath.
22.....	Northeast station	5	1.5	Brown, fibrous peat; mostly cranberry, sphagnum, and sedges.
26.....		18	5.4	Granular peat; very sandy above, marly beneath.
27.....		28	8.4	Sandy marl; blue clay beneath.
28.....	Southeast station	5	1.5	Brown, coarse fibrous peat.
29.....		10	3.0	Dark brown, slightly fibrous; a lighter colored coarse fibrous peat underneath.
30.....		20	6.0	Brown, fibrous peat containing roots and rhizome fragments.
31.....		40	12.0	Black, plastic, non-fibrous peat; bottom not reached.
32.....	Southwest station	5	1.5	Light brown, coarse fibrous peat.
36.....		20	6.0	Plastic, fine fibered, dark brown peat containing shell marl.
38.....		40	12.0	Black, plastic, non-fibrous peat; bottom not reached.
40.....	Northwest station	5	1.5	Light brown, fibrous peat, composed of sphagnum and other bog plants.
42.....		20	6.0	Fine fibered, dark brown peat.
45.....		28	8.4	Sandy gravel underlain by blue clay.
48.....	Lake station	6	1.8	Dark brown, slightly fibrous peat.
49.....		40	12.0	Black, plastic, non-fibrous peat; bottom not reached.

It will be seen that the accumulation of vegetable matter has been sufficient to cause the lake basin to be filled with a layer of peat of considerable depth. The deeper strata have been reduced by humification, largely to the form of a black humus, a semi-liquid muck. The fineness of grain and the peculiarly soft consistency of it suggest that it is in part made up of the remains of algae, and in part a filling from the border of the lake, spread over the bottom. The upper strata are lighter in color, and very fibrous, loosely felted in structure, and have a matted appearance. As the island is sounded through from top to bottom, the samples brought up show a progressive change in color from light to darker shades, and in texture from coarse and loose to fine and more compact peat always saturated with water. In some places this sequence is repeated, that is, below the peat muck occurs a second fibrous brown layer followed by muck or clay. The escape of gases is very noticeable during the test borings, and also the staining of the brass peat sampler to a bluish-purple bronze, indicating the presence of a gas like hydrogen bisulphide. Only a small deposit of shell marl has thus far been found underlying the peat substratum in places. The Characeae and Cyanophyceae concerned with this process (**10**) are not abundant enough to be considered as agents in the aggradation of the basin. The lake bottom is of clay and in places somewhat sandy. The thickness of the deposit of peat in this morainal depression indicates, therefore, that the vegetation must have obtained an early foothold.

The chemical analysis of the substratum

The drainage of the bog island is merely that due to seepage through the porous peat. Ordinarily very little water passes either into or out of the bog island, except at such times when the water level of the lake fluctuates with extremes in precipitation or from interference in drainage. Even then the seepage is not rapid. The amount of salts dissolved in the lake water which is retained by absorption in the humus soils along the margin of the bog island is relatively small. The analyses show a total mineral content of 4 and 9 parts per hundred for the central and marginal zones respectively. Average samples of the air-dried peat taken

at a depth of one foot (30 cm.) from the surface layer give the following chemical composition (table II). For purposes of comparison analyses have been added of peat soils from a tamarack bog near Edgerton, Ohio (station VII), from a bog near Orrville, Ohio, now under cultivation in celery, onions, etc. (station VIII), and from a peat bog under cultivation, the soil of which is reported as unproductive (station IX).

TABLE II

CHEMICAL ANALYSES OF PEAT SAMPLES

Constituents	Sphagnum-cranberry zone	Maple-alder zone	Tamarack zone	Cultivated peat	Diseased peat
Volatile matter	60.90	68.91	60.50	52.47	52.56
Fixed carbon	22.19	19.60	26.84	23.98	19.35
Ash	7.68	3.56	3.30	14.70	19.42
Sulphur	0.12	0.00	0.20	0.39	2.21
Nitrogen (equivalent to ammonia)	0.80	2.55	1.51	2.58	2.38
Potash (K_2O)	0.12	0.12	0.15	0.31	0.64
Phosphoric acid (P_2O_5)	0.03	0.03	0.29	0.34	0.37
Insoluble	0.00	0.00	0.15	0.07	0.15
Available	0.03	0.03	0.14	0.27	0.22

It appears, therefore, that where peat varies from a highly fibrous condition, light brown in color, as in the sphagnum-cranberry zone, to a structureless condition, i.e., well decomposed, only slightly fibrous, and dark brown in color, as in the maple-alder zone, not only the physical constitution but also the chemical composition is highly variable. The determinations, which were made in the same way as fertilizer analyses, show conclusively that from the standpoint of available plant food constituents, the peat of the maple-alder zone is superior to that of the central sphagnum-cranberry zone. The analyses of peat ashes indicate only a small fraction of a per cent of potash and of phosphoric acid, but a fairly large amount of the valuable nitrogen ingredient. Preliminary work indicates also that the relative availability of the peat nitrogen seems at the most 8 to 12 per cent; but that this relative availability of peat nitrogen is considerably increased when the peat is composted with the bacterial life from stable manure, the peat from the central sphagnum-cranberry zone dis-

integrating, however, less readily than that from the maple-alder zone.

The reducing action of peat soil

It is a well known fact that fresh samples of bog soil upon exposure to the air extract oxygen from the air with great rapidity. Soil-sampling tests show that this power is strong in the cranberry-sphagnum peat, reaches a maximum in areas where the peat substratum is compact and less coarsely fibrous, and decreases as the border zone along the margin of the lake is reached. Judged by the quickness with which the soil becomes colored, and the intensity of the color, reducing processes increase on Cranberry Island from any marginal point to the central zone, and decrease as the opposite shore is approached. Reduction action becomes greater with the depth of the deposit.

The reducing power of the soils is shown clearly by the addition of a starch iodide solution. The observable action is variable, as already mentioned; the blue color disappears rapidly in soils from the cranberry-sphagnum area; the solution is greatly lightened with soils nearer the margin of the lake; no action is detected with soils along the margin. Various dyes such as lacmus and methylene blue and other coal tar colors decolorize similarly. Possibly the absence of sulphur in the analysis of maple-alder peat (table II) is due to the complete conversion of sulphur to hydrogen sulphide. This gas is the product of a reduction and has been detected by means of lead acetate paper.

Whether the reduction power in peat soils is produced by microorganisms, is due to enzymes, or caused by external chemical or bacterial metabolic products, these tests fail to show. Nothing absolutely certain is known regarding the composition and the nature of reducing substances. They have not at present been very fully studied by ecological workers. Apart from their destruction by aeration, tillage, and heat, and their adsorption by insoluble substances such as quartz, kaolin, carborundum, lamp black, and others, uncertainty exists as to whether the reducing bodies in bogs are unsaturated compounds comparable in properties to unsaturated fatty acids, to substances which possess the characteristics of certain organic reducing ferments, or to

residual by-products of an incomplete disintegration of peat. They unquestionably reduce oxygen-containing compounds in contact with them; their action is most marked where micro-organisms play a part in decomposing organic matter; the amount reaches, it seems, a maximum in early autumn. It should be stated further that toxicity and the reducing action of peat soil and that of the decomposing organic matter which retards oxidation in the soil are not necessarily the same phenomena. An increase in the amount of oxygen does not always decrease toxicity or the reducing power of the soil, and hence the amount of oxygen absorbed cannot be taken as the measure of the total action of these conditions.

Reduction processes are predominant in the early stages of peat formation, but are less manifest as the concomitant plant societies are succeeded by others, and especially when deciduous forests prevail. The same factors which decrease the toxicity of the habitat and the accompanying reducing processes favor an increase in the rate of oxidation and influence thus the character and nature of the succession. The greater oxidation, therefore, in the known productive peat soils would seem to be due to the activity of a different set of microorganisms, which by enzymotic action or otherwise hasten the formation of compounds of an assimilable nature. The excessive oxygen avidity of peat soils in the early formation stages must undoubtedly be injurious to plants, unless the plants, indigenous or invaders, are likewise able to exhibit oxidizing or reducing powers. The reducing processes in a soil very likely activate oxidative powers in plants. The various reactions of fungi, micorhiza, alder tubercules, bacteria, and the roots of higher plants growing in peat and humus soils should on that account be made the subject of considerably greater and more detailed study. The consideration of the relation between plant societies, relative physiological aridity, and micro-organisms, with their reductive and oxidation processes in soil has scarcely passed beyond the theoretic field of speculation. And yet it is this relation which makes soil problems especially interesting and in need of experimental work of considerable scope (**28**).

The bog water is relatively clear, the suspended particles imparting to it a slight tinge of olive green to brown. The analysis of samples of bog water and lake water give the following results (table III).

TABLE III

CHEMICAL ANALYSIS OF BOG WATER AND LAKE WATER FROM CRANBERRY ISLAND

Constituents in parts per million (May 30, 1910)	Bog water, central zone (cranberry-sphagnum)	Lake water
Nitrogen as albuminoid ammonia	10.34	4.50
Nitrogen as free ammonia	5.19	2.95
Nitrogen as nitrites	0.0005	0.0000
Nitrogen as nitrates	0.20	0.10
Chlorine	0.30	1.00
Required oxygen	71.80	3.70
Alkalinity (as $CaCO_3$)	30.00	75.00
Incrustants (as $CaCO_3$)	74.00	76.00
Total solids	140.00	200.00
Loss on ignition	100.00	4.00

Examining these results, shown in table III, we find that the lake water contains organic matter in a state of advanced decomposition. This is indicated by the relatively high free ammonia, and the small amount of oxygen consumed. The reverse holds true for bog water from the sphagnum-cranberry zone. In other points lake water agrees well with bog water. The osmotic pressure and the acidity have been found to be the same for both stations. As compared with the freezing point of pure distilled water, the average lowering in the various determinations is 0°.007 and 0°.009 for the central station and the maple-alder and lake station respectively. Acidity varies from less than 0.00075 to 0.0038 normal acid when titrated with a $n/0.05$ NaOH solution. The soil is alkaline at depths near the marly subsoil. The stress laid by various authors upon the relation of these two factors to plant societies in bogs, in so far at least as this region is concerned, will not hold. They are not factors in the selection or distribution of species for bog habitats.

Physiological properties of bog water

The physical and chemical sides are found unsatisfactory to explain the functional variations and the pathological changes

in structure which agricultural plants undergo when growing in peat and bog water. Elsewhere it was shown by means of transpiration data of cultivated plants, and with a biometric study on the annual wood-increment in the red maple found on the island and in woodlots near the shore, that (1) a difference exists between different species in their power of resistance to the toxic action of the substratum; (2) the contrasts in the relative growth of plants vary with the substrata of the several bog plant formations; (3) the toxic principles whether enzymes or other bodies are not found in bog water when attempts are made to extract them with insoluble adsorbing bodies; they do not pass readily through filters and only slightly through filter paper; (4) different physiological phases result from the progressive addition of an adsorbing substance; (5) agricultural soils used as filters decrease considerably the normal physiological activity of plants growing in them; (6) the reduced absorptive capacity of the plants is not a consequence of the absence of root hairs, or of a smaller absorbing surface.

The bacterial flora of the peat substratum

Present writers seem to hold the view that among the simplest of fungi, the Schizomycetes, few are present in peat bogs, and that only a small number of species, included in perhaps only one family, are at all injurious to higher plants. Examination has shown that peat soils contain unsuspected groups of bacteria, which in number and efficiency vary during the seasons and with the several plant zones on the island. As a means of differentiation between the bacterial flora of the plant formations, studies were made on the action of the bacteria in 0.5 cc. bog water upon various culture media in fermentation tubes. Soil water solutions were collected in sterilized glass-stoppered bottles from each of the following stations: station I, lake water; station II, marginal zone (*Decodon-Typha-Hibiscus*); station III, cranberry-sphagnum zone, 1–3 feet; station IV, same, 3–5 feet below surface vegetation; station V, maple-alder zone, 1–3 feet; station VI, same, 3–5 feet below surface vegetation; station VII, tamarack soil from Edgerton, Ohio; station VIII, peat soil under cultiva-

tion from Orrville, Ohio; station IX, peat soil under cultivation, reported as unproductive and "sterile," from Lodi, Ohio; station X, humus soil from the university woodlot (beech-oak-maple-elm). The culture media employed for this work were a 1 per cent starch peptone water solution; 1 per cent solutions of cane sugar, dextrose, and lactose in beef broth; plain bouillon; plain and litmus milk; 0.2 per cent nitrate peptone water; Dunham's peptone solution for the indol test; nutrient gelatin and agar. Only the generally well known determinations, as of the breaking up of carbon and nitrogen compounds and the proportion of the various gases evolved, have been made. The chemical analysis of the soil samples of stations I to IX is given in tables II and III.

The culture studies gave the following characteristic results after an incubation period of 5 days at 38° C. The action of the bacteria on starch shows in several stations the production of an inverting ferment by the cultures. The starch is changed into a sugar which reacts with the Fehling's test. In stations III and IX there is no action; in stations II and X the conversion is carried on a little way and then stops, there being always a red or purple reaction with iodine; in station I the starch conversion is almost complete; while in stations IV, V, VI, and VII certain putrid by-products inhibit in various degrees further conversion. Upon the addition of a few drops of potassium iodide, the blue color disappears rapidly in stations III, IV, and VI; the hydrated iodine is deposited as metallic iodine upon the walls of the test tube above the solution. Reduction action is less active in stations V, VII, and IX. No decolorization occurs in stations I, II, and X. The accumulation of iodine is very strong in the test tube of station X and is very likely an indication of the presence of oxidizing ferments. With methylene blue the reduction action is the same in degree, respectively, in all cases running parallel with the iodine action.

In all stations, with the exception of station I, the action of the bacteria on saccharose shows both the conversion of the carbohydrate into glucose by the inverting ferment, and the production of gas and acid. The reaction is strongest in stations VIII and X; relatively small in stations V and IX; very little gas is evolved

in station II. The gas is largely hydrogen gas and CO_2; the latter, with the exception of stations V and VIII, is present usually in small quantities and was distinguished from other gases by its absorption in sodium hydroxide. Fermentation action is shown better on dextrose and lactose. There is little growth and gas formation in station I; no acid is produced in stations VII and IX; and very little hydrogen gas is formed in station VIII. In all cases the growth of the organisms produces a marked and varied pigmentation in the solutions.

In plain milk, rapid coagulation precedes further bacterial action in all cases except station IX, in which coagulation occurs very slowly. Milk is slowly peptonized anaerobically in stations IV, V, and VI; surface digestion takes place in stations III, VIII, IX, and X; it is rapid in stations I, III, and VI; and gas is produced in moderate quantities in all stations except station VIII. Litmus milk is coagulated in all stations; the medium gradually decolorizes and the cultures become acid in various degrees; the color does not return upon steaming the test tubes. With a majority, gas is produced in various amounts during digestion, except in station IX, in which the bacterial reaction is faint though strongly odorous.

On bouillon bacterial growth is slow; it is never very turbid or heavily clouded, and only in one case, station IX, gives a whitish precipitate.

The power of indol production is greatest with the organisms in stations III, V, and IX; the action is relatively small in stations II, IV, VI, and VII; and present to a feeble extent only in stations I, VIII, and X when tested with 0.02 per cent solution of potassium nitrite and sulphuric acid.

The ability to form nitrites from nitrates in nitrate broth is common to the organisms in all stations. The amount of nitrites formed is high in stations IV, VI, IX, and X, and very small in stations I, II, VII, and VIII. The power to reduce nitrates to nitrites is not present in the same degree as noted above for the reduction action in starch media. It is certain that the microorganisms are capable of reducing nitrates, but to some extent metabolic products, apparently, modify the action. The test

was made with equal parts of sulphanilic acid and napthylamine solution.

The presence of ammonia was tested with Nessler's reagent. The reaction is stronger in stations VII and X than in any other station. A faint test is obtained in station IX. Nitrogen gas is produced from nitrates in stations VII and VIII.[2]

Before summarizing the facts brought out in the culture studies, there is need of mentioning another matter. A knowledge of the morphology of the simple form of organisms does not suffice to differentiate the numberless more or less similar species. It is difficult and almost impossible to identify a distinct and constant type for each species, or recognize form-differences suitable for classification. Nor does it seem that culture methods have made possible systematic grouping, or the variety of tests needed for accurate and trustworthy comparisons. No necessity exists for doubting the value of cultural characters; it is merely maintained here that additional and new methods must be tried, and tests should be scrutinized from every standpoint. Though widely different in their behavior in culture media and in their relation to air, yet the pathogenic properties of the bacterial flora from the different plant formations and societies should be ascertained within the limits of their natural habitat, and should be determined also with reference especially to the degree of functional inhibition on higher plants. It is not until a study is made of the special reaction of bacterial transformation products in sterilized bog water upon the growth of agricultural plants that the lack of salient features between habitat relations and physico-chemical reactions in artificial media becomes noticeable. Considerable difficulty was experienced in the isolation of organisms with the conventional media. In the majority of cases very little growth was obtained on beef broth gelatin or agar. Gelatin and agar media made with peat and bog plant juices proved more satisfactory for isolation purposes. Moreover, bacteria of rapid growth and early appearance of colonies on the artificial media

[2] Since the observations herein recorded, the writer received through the courtesy of Professor HARSHBERGER a paper published by Dr. D. RIVAS on "Bacteria and other fungi in relation to the soil" (Univ. Penn. Publ. **3**:243–274. 1910). It is cited here as bearing directly on the problem in hand.

caused less retardation on the growth and transpiration of wheat plants when inoculated into sterilized bog water than bacteria of slow growth. In some cases the isolated pure cultures made little headway on beef broth or peat agar media after a period of 3–5 months, but gave strong inhibition in the growth of wheat plants within 3 weeks after inoculation into sterilized bog water from their respective plant zones. It is reasonable to assume, therefore, that the lack of uniformity in results implies both obligative symbiosis and the need of a physiologically balanced culture medium. The fact that the organisms are obligate saprophytes, capable of growing only on substrata similar in composition to the character of the surface vegetation, is indicative of a close interdependence; their rapid growth in a medium in which cellulose and lignin compounds predominate suggests a specific cytohydrolytic action. Certain microorganisms in station III have been found to possess the ability to dissolve filter paper, but their isolation has not been successful.

It is needless here to repeat the physiological tests which were made with a number of isolated pure cultures inoculated in sterilized bog water. Transpiration figures of wheat plants growing in these solutions and various other data have been published in an earlier paper (*l.c.* 9) to show the active participation of the organisms in the formation of bog toxins, and their ability to inhibit during the processes of denitrification and dehydration the growth of plants alien to the habitat. With these suggestions in mind, the results on the bacterial reactions in culture media submitted above may now be summarized as follows:

Peat soils are very rich in bacteria inducing diastatic, inverting, proteolytic, cytohydrolytic, and reducing action.

The organisms vary in kind and number with the nature of the substratum.

The majority of the forms are found to thrive as saprophytes, digesting the débris in the upper layer of the peat substratum and aiding in a partial disintegration of the accumulating deposit. Many forms thriving as saprophytes among the indigenous flora give little aid in the elaboration of food materials to invading or introduced plants.

The organisms show a marked interdependence between themselves; one set of bacteria prepares a medium for another out of an unfavorable substratum, and this paves the way for others to continue the destruction. Signs are not lacking, however, of relative indifference and even antagonism among the organisms, resulting in products which retard and inhibit further bacterial growth and disintegration processes.

A certain proportion of bacteria in these soils has the special ability to produce substances, perhaps unassimilable, certainly injurious to all but indigenous plants. In a peat substratum the percentage of bacteria aiding in the production of deleterious substances such as reducing bodies, gases, indol, and other fermentation products varies with the season of the year, but especially with the advance of the vegetation toward the closed deciduous forest formation. These bodies constitute the unsanitary conditions in soils, the negative factor which limits the rate at which the splitting up of organic compounds into ammonia and other assimilable substances proceeds. They are the characteristic symptoms of a diseased, sterile soil. The greater oxidation in the productive peat soil is due to the activity of a different set of bacterial organisms. The rôle which microorganisms play in the soil points, therefore, to the fact that among other things a considerable relation exists between the processes of disintegration of organic material and the succession of plant formations in bogs and marshes, and in peat soil under cultivation.

Each plant formation has its own bacterial flora maintaining a physiologically balanced condition in the soil. The substratum of each plant formation is an ever varying medium, the seat of physical, chemical, and vital activities which directly and indirectly influence its relative fertility and the character of the surface flora. Varying with the power of multiplication and metabolic activity is the quantity of the products of decomposition constituting a toxic, physiologically arid habitat at one phase, and an available supply of nutrients to plants at another stage of the process. Acidity, toxicity, and reduction action represent merely a stage in the decomposition of organic matter. In the natural successions which ensue, each plant association augments the

efficiency of the soil as a habitat. The soil processes involved are an efficient natural process for the maintenance of relative productivity. Differences in the mineral components are trifling compared with the biological processes.

The sum total of the reactions in any stage of the process exercises a physiologically selective function upon invading plants, furthering the growth of such plants whose roots are not merely absorbing organs, and excluding and eliminating all others in which the power to make extracellular changes in the soil is inefficient.

The significance of the data calls, however, for still further experimentation to be of sufficient evidence to assume a specific metabolism in bog plants, or to disclose the chemical nature of bog toxins.

Origin of the habitat

Initially the bog island was formed as are all bogs occurring in glacial moraines, or in depressions which form frequently in the gravel plains along the lines of drainage from the front of the glacial ice. Extensive acquaintance with peat bogs or a comparative study of the lists of plants from different regions will convince any careful observer that bogs are very different in character, and that not all of them have been formed in the same way. There may be a number of possible ways by which such accumulations of vegetable matter came about. Various such points of view and methods of classification have been suggested in a comprehensive study by DAVIS (11). As the process of bog development here seems similar to that of the peat deposits which the writer has observed at Michigan, the following brief account is given.

During the glacial period, most species common to bogs skirted the border of the ice sheet. Whatever plant or animal life existed was confined to the highlands east of the Scioto Valley, south of the Ohio River, and in the southern portion of this continent. At the margin of the ice sheet the conditions must have been quite circumpolar in character, similar to those of the barren grounds of the far north, that is, there prevailed short summers and long winters with frequent winds and storms. Whatever the causes

that resulted in such climatic conditions (4) with their change and with the progressive northeastward movement of the ice, an increasing land area became exposed, the topography of which is even now largely the inheritance of that time. While yet the entire surface of northern Ohio and the land north of it was buried under the ice sheet, the region about Columbus and Buckeye Lake was among the first to be laid bare by the retreating ice and water. The receding of the ice sheet was paralleled by the northeastward movement of more favorable weather conditions which initiated a migration northward of plants and animals along the glacial drainage channels, the earliest highways for the dispersal of many forms of life (1). As the ice and water continued to recede and the processes of erosion brought about better drainage and lower water levels, the flora and fauna followed down the slopes and began to encroach upon the ponds and lakes. The bog plants and their associates slowly had passed northward close to the base of the retreating ice, and hence were among the first to take possession of the new territory.

As has been stated, the test borings make it evident that the bog vegetation grew out from the shores, forming a floating mat; that sphagnum and cranberry appeared after the sedges and rushes had built up the surface mat; that filling in of débris from the sides continued slowly until the water had become shallow enough in places to enable shrubs and trees to occupy the area. The later phases of mature bog forests the writer has met very frequently in Ohio, and several interesting localities have been studied in connection with an inquiry on the peat deposits made for the Ohio Geological Survey.

While it is not clear how the preservation of the local bog island has come about, the present investigation has led to the conclusion that a well marked relationship existed between the type of peat soil considered with regard to its degree of disintegration, and the succession of plant associations covering it. As elsewhere in Ohio today, the firmer and well decomposed peat strata were covered sooner with forests, and were built up rapidly by an attendant sinking and shrinkage of the mat under the added weight of the growth and fall of trees and the vegetation of suc-

cessive seasons. On the other hand, the absence of logs and fallen timber in the peat of the sphagnum-cranberry zone points clearly to a relatively slow encroachment upon the open water by the plants. When inundation took place, only the coarsely fibrous and incoherent cranberry-sphagnum mat rose with the water level, and its vegetation survived.

As late as 1830 the bog was an extension from the mainland. After the formation of the dike, and the consequent rise of the water level, most of the mainland became inundated, leaving the bog completely an island. With its surface vegetation of mostly northern forms, the island is virtually a water culture on a large scale. None of the plants are dependent for any important part of their food on the mineral soil below the peat. Cranberry Island is, therefore, not to be considered merely as a case of the conversion of a forest into a marsh under the influence of an increased water content in the soil. The analysis of peat samples shows that the vegetation now growing upon the peat substratum represents quite fully a continuation of the former boreal flora. It presents today a somewhat disjointed distribution, but this has come about chiefly through recent repeated disturbances in the water level of the lake, through a settling and shrinkage of the peat soil, through the slow encroachment of the invading southern vegetation, and through the formation in places of a better and firmer soil.

The flora

For convenience three well marked plant zones may be pointed out, each of which is characterized by communities and groups of plants easily differentiated from the others. No attempt has been made to give full lists of plants, or to correlate the associations and successions mentioned with similar conditions elsewhere. Essentially the same order of succession and of arrangement of plants as has been described for northern bogs is not, of course, to be expected. The species are not always the same in the corresponding formations, but they are systematically related and closely similar in ecological structure.

A fuller floristic treatment is now in preparation, in which many of the features are described in detail.

THE BORDER ZONE

The outermost growth which immediately borders the open water and forms a more or less broken fringe around the island is for the most part hydrophytic. Along the southern shore it is dominated by the swamp loosestrife (*Decodon verticillatus*) and in places by cat-tails (*Typha latifolia* and *T. angustifolia*). This facies has for its principal and secondary species *Hibiscus Moscheutos*, *Sagittaria latifolia*, *Polygonum hydropiperoides*, *Ranunculus pennsylvanicus*, *Scutellaria galericulata*, *Lathyrus myrtifolius*, *Bidens cernua*, *Potentilla palustris*, *Campanula aparinoides*, *Galium triflorum*, *Cicuta bulbifera*, *Peltandra virginica*, and others. They are generally abundant, with *Decodon* and *Typha* forming a dense growth, which attains a height of 2–6 feet (0.6 to 1.8 m.) above the substratum. The vertical zonation is that of the differences in habit of growth of the individual species. The members differ widely from one another both in external features and in their demands upon the environment. In these regards the vegetative shoots adapt themselves little to the prevailing exposed conditions. Growing upon a peat substratum whose depth and physical characteristics are in every way like that of the other plant zones to be described below, the xerophytic type and quality are least marked in this vegetation. The well decomposed peat soil of the border zone permits here a luxuriant growth. The plants are able to secure all of their raw food materials from the water and air, and build their own substratum. The high water capacity of peat, the absence of a mineral soil, the smaller percentage of oxygen in the water, and the incoherency of the substratum afford no precarious conditions for growth. Here the toxicity of the substratum and the consequent physiological aridity are least marked. It is evident that dilution and the capacity of absorption of soluble salts by the humus soil along the margin (**8**, p. 403; **9**) corrects any harmful effect.

The *Decodon-Typha* association has a transition appearance, for a considerable admixture of plants such as *Rosa carolina*, *Cephalanthus occidentalis*, *Cornus canadensis*, *C. paniculata*, *C. stolonifera*, *Salix discolor*, *S. nigra*, *S. pedicellaris*, *Alnus incana* (?), *A. rugosa*, *Ilex verticillata*, *Prunus melanocarpa*, *Rhus Vernix*,

and various secondary dependent associates, occupy the firmer parts of the marginal zone and form an almost continuous fringe, the *Alnus-Rhus* association. In places it extends diagonally across the bog island as scattered dense thickets (fig. 4). This community of plants presents on the whole very little zonation within itself. It constitutes a zone of varying width, 5–30 feet (1.5–9 m.) and more, and attains a height of 8–12 feet (2.5–3.5 m.). Only in a few places along the southern shore this type of bog shrub formation is absent altogether and is replaced, as has been

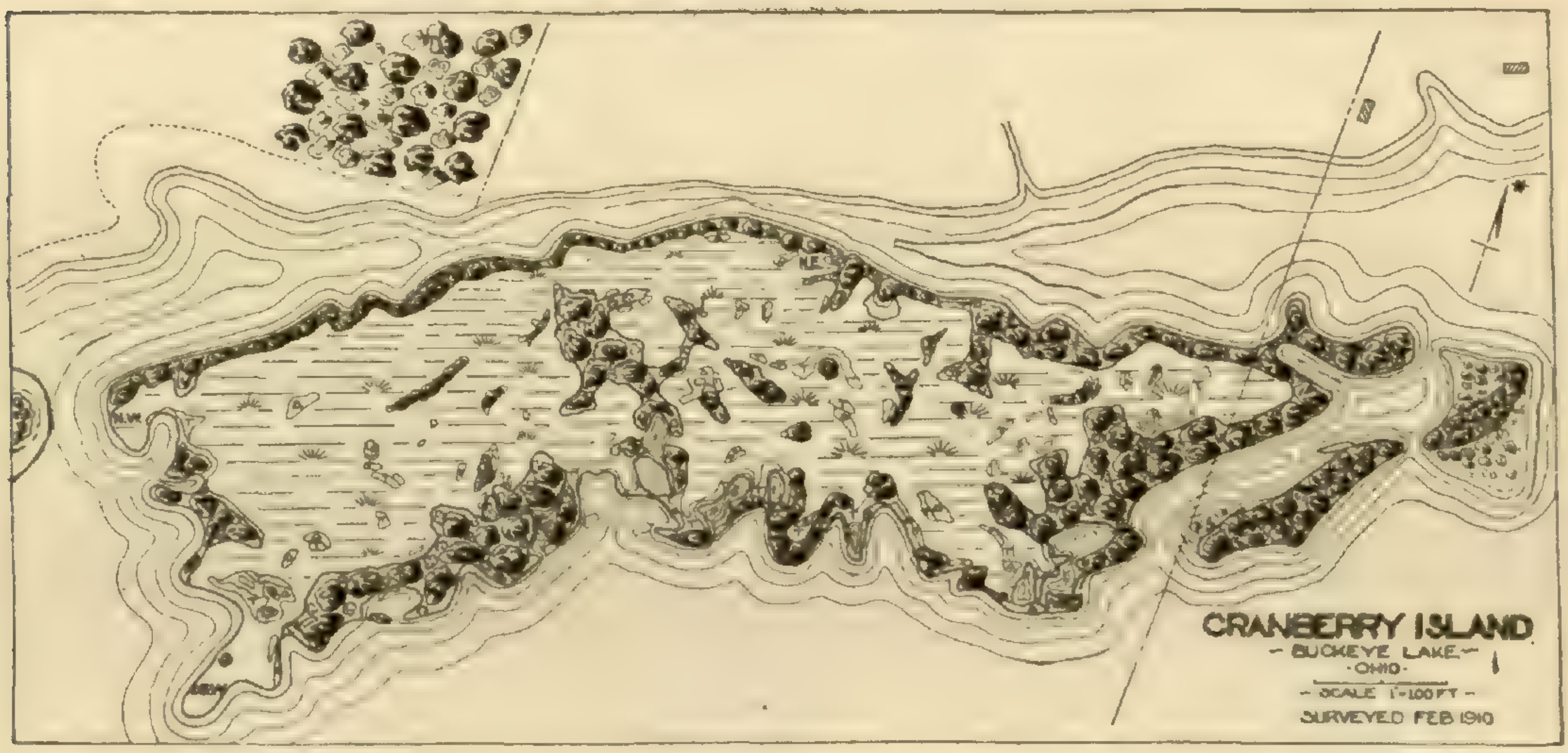

FIG. 4.—Map of Cranberry Island; surveyed February 1910; the divisions into plant societies as indicated by the map and the text are based on general characters of the vegetation; Δ, *Decodon;* *T*, *Typha;* the ponds on the island are shaded.

stated, by *Decodon* and *Typha*. The edaphic conditions of this part of the habitat seem to approximate those of the undrained swamps as described by COWLES (**6**). Nearer the lake there is a tendency toward the segregation of *Decodon verticillatus* and *Hibiscus Moscheutos*. Of the two, the former is more vigorous and occupies the deeper water. *Rosa carolina* prefers the outer border also, but clings quite closely to *Alnus incana* and *Cornus stolonifera*. Contemporaneous with the thicket-formers, various species of lianas invade the association. The mature thickets are often covered with an impenetrable growth of tangled vines of *Apios tuberosa*, *Solanum Dulcamara*, *Convolvulus Sepium*, *Ipomoea* sp., and *Cuscuta Gronovii*. *Cephalanthus occidentalis* does not

constitute a large part of the shrub formation. Together with *Decodon*, it is found frequently indiscriminately mixed with facies in the central zone. In fact, the differences in the formation are to be seen largely in the ratios between the numbers of individuals present, and not in their entire absence from either.

THE MAPLE-ALDER ZONE

With the maturity of the facies, a gradual change in the environmental conditions for the plants takes place. The annual leaf-fall covers the substratum with a visibly thicker layer of vegetable material rich in organic matter, and is followed by the growth of fungi and bacterial organisms favorable to succeeding plants through the formation of available nitrogen. Like snow and ice, the covering of fallen foliage reduces the extremes of soil temperature, suppresses the growth of *Sphagnum*, *Oxycoccus*, and similar plants from the adjoining central zone, and improves the production of a kind of humus of great significance to the animal life as well. Moles, earthworms, snails, and insects are not uncommon in this zone. The shade of the trees during summer and autumn checks extremes in evaporation, and thus reduces the transpiration from the herbs and shrubs beneath the trees. Through the combined action of these and various other agents, there is a corresponding rearrangement of some species and the disappearance of others. In places along the margin, the peat substratum is firmer, fairly well above the level of the lake, and comparatively better drained. These conditions are sufficiently established at the southeast side of the island to be characterized as the maple-alder zone. The bog tree formation is quite prominent, and though not extensive, it is still a strongly marked zone. The most conspicuous plants are large-sized maples (*Acer rubrum*), alders (*Alnus incana*, *A. rugosa*, *Ilex verticillata*), the chokeberry (*Prunus melanocarpa*), black cherry (*Prunus serotina*), and poison sumach (*Rhus Vernix*). Oaks (*Quercus palustris*, *Q. imbricaria*), ashes (*Fraxinus nigra*), and the silver maple (*Acer saccharinum*) are still relatively rare. The trees are surface-rooted. The roots do not penetrate to a depth of more than one foot (30 cm.). They spread out in all directions from the trunk, and are of sufficient

size and length to withstand the mechanical strains due to the action of air currents. The association is still an open community of plants and has four distinct vertical layers. The trees cast a relatively dense shade, in which grow seedlings and young trees of oak and maple, and a variety of shrubs and herbs. Most abundant are *Sambucus canadensis*, *Impatiens biflora*, *I. pallida*, *Rubus* sp., *Dianthera ovata*, *Viola blanda*, *Aspidium spinulosum*, *Osmunda regalis*, *Carex scirpoides*, *Aspidium cristatum*, *Habenaria clavellata*.

There is protection from strong air currents, and in the changed light, heat, and moisture conditions the plants offer a striking contrast to the vegetation next to be described. Many of the herbaceous and shrubby species occur only sparingly, and are really constitutents of the other societies of the border zone. In the numerous maple and oak seedlings the evidences are seen that the *Rhus*-alder consocies will not continue to occupy the habitat. The lowering of the water table due to the continued addition of débris and leaf-humus will hasten the advent of better soil, drainage, and shade conditions. *Alnus* and *Rhus* and their associates will find the new conditions unsuitable; they will disappear, leaving the zone more typically an oak-maple-ash formation. It is not probable that this coming society represents a climax forest for filled lake basins in this locality. There are limited portions on Cranberry Island which in the course of years are bound to revert to the central zone bog type, and that perhaps intermittently, for a settling and shrinkage of the numerous water pockets in the peat substratum will continue until all of the lower strata have become firm and compact. With continued accumulation of forest litter, the soil conditions will finally become drained and more xerophytic, to an extent that will constitute an ecological habitat considerably different from that existing in the neighborhood. Should the water level remain constant, the amount of upbuilding will be limited to the distance to which the water will rise through the accumulation of peat, and supply the growing plants at the surface with the necessary physiological water. It must not be assumed, therefore, that the development of a mesophytic forest could continue in the same direction indefinitely.

It is the lack of moisture, and not low temperature that will arrest the growth and reproduction of the plants concerned, and the disintegrating action of fungi and bacteria. This factor in plant growth, not previously important to the plants of the sedge, shrub, and thicket growth, then becomes operative selectively, leading to the establishment of a xerophytic plant association. At present, however, there is little indication of the appearance of an association of that kind; the climatic trend favors broad-leaved forests, and the supposed physiographic characteristics leading to a xerophilous climax association assume nowhere on the island any considerable importance.

There are conditions, however, which would indicate a reversion to a hydrophytic association. Adjoining the maple-alder zone on the southeast side are several extensive areas which do not respond quickly to changes in the water level; fig. 7 illustrates a part of such an area. Through the accumulation of vegetable débris, the replacement of air and other gases held in the mat by water, but especially through the increased load upon the surface of the mat after the heavier tree association became established, a settling and shrinkage of the peat occurred, which ultimately resulted in the sinking of the mat several feet below the water level. The cutting of the timber reestablished equilibrium and rejuvenation. The species now tenanting the mat indicate a tendency toward the development of a hydrophytic vegetation approaching the type of the border zone described. The marked difference between the vegetation of the central zone and the one establishing itself is worthy of special note. Except such portions of the fibrous mat as were long ago broken off from time to time by the action of wind and waves and drifted about as floating islands, the rejuvenated "sunken" mats, and such areas as annually rise in the early summer and disappear again beneath the water in late autumn concomitant with the "overturn" of the lake, show nowhere members of the cranberry-sphagnum zone. They illustrate most forcibly the fact that under these conditions a very different set of plants spring up and become dominant, although the true bog plants are near at hand.

THE CENTRAL ZONE

This zone is situated centrally on the island. It occupies the larger part of the area of the island, and in its floral structure is very distinct. The plants consist principally of *Vaccinium* (*Oxycoccus*) *macrocarpon* and several species of *Sphagnum*, with *Rhynchospora alba*, *Eleocharis obtusa*, *Aspidium Thelypteris*, *Dulichium arundinaceum*, *Carex comosa*, *Scheuchzeria palustris*, *Juncus canadensis*, *Eriophorum virginicum*, *Osmunda cinnamomea*, *Drosera rotundifolia*, *Menyanthes trifoliata*, several orchids, and other light-demanding forms variously grouped. The surface is characterized by hollows and elevations. The latter are due, in the opinion of the writer, to various causes; in part to the upward growth of sphagnum competing with cranberry, in other places because of a mutual protection which is afforded by the massing of forms of a similar height against excessive loss of water. In still other places, cranberry and sphagnum are growing beneath shade-producing forms, notably around ferns and invading maples and sumachs. Here they possess the ability to grow up in a manner giving rise to a thick soft mass, raised to a considerable height, more at the center than at the periphery. The maximum height to which cushions of sphagnum can grow is limited by the vertical saturation gradient of the water content in the air. The vertical level of this vegetation is otherwise fairly uniform, and varies only between 6 inches (15 cm.) and 1.5 feet (45 cm.) above the peat substratum, forming a low, dense, compact growth. The taller growth of grasses and sedges and the occasional bushes of *Gaylussacia baccata*, *Prunus melanocarpa*, and *P. arbutifolia* occur chiefly scattered and as open facies. They do not dominate the general vegetation enough to interfere with the transpiring organs of the plants at the lower level.

A more detailed study of the distribution of the species in the lower stratum shows habits of growth giving rise to vertical layers sufficiently defined to recognize vertical zonation; especially the differences of growth in height in the sphagnums, *Gaylussacia*, and *Vaccinium* in areas of varying physiological aridity show that the plants are adapted to a given average supply of water. But

in the zone under consideration, the differences in habit of form shade into each other, and in consequence are less distinct than those in the adjoining border zones. The prevailing grasslike growth-form, the general reduction in size of leaves assumed by the different species, is in harmony with the environment. It expresses itself not only in external features but also in the anatomical structure. As an ecological unit, the community of plants, identical in type, but different in floristic composition, exhibits well within itself the impress of its conditions of life.

FIG. 5.—A pond in the cranberry-sphagnum association; *Decodon* is the most important mat former making the advance upon the water.

Differences in aerial functions would be therefore largely species characteristics as well as environmental.

That the plants are adapted to a given average supply of available water, but with great specific differences among themselves, is further seen in the frail growth of *Cephalanthus* and *Decodon*, in the small trees of *Acer rubrum* and *Rhus Vernix*, and in the stunted forms of various other invaders from the neighboring plant societies which occur scattered throughout this zone. For the past few years thousands of maple, sumach, and alder seedlings have been observed to sprout, and yet failed to succeed beyond the first year's growth. Of those which succeeded, the stunted growth, the numerous dead branches, the ragged crown of foliage,

are a clear instance of the fact that the resistance offered by the invaders to the toxic conditions of this habitat is, indeed, but slightly effective.

There are several small ponds in the cranberry-sphagnum zone in which the dominance of *Decodon* and *Typha* as important members of the border vegetation is especially to be noted (fig. 5). *Decodon* is particularly well adapted in making an advance out-

FIG. 6.—The last stage of a larger water area, now occupied by the advancing cranberry-sphagnum association.

ward upon the water by the manner in which the slender mature stems, that bend toward the water, curve at the tips. From the submerged part roots arise in considerable numbers, buds form, and new plants develop. The young plants remain moored to the parent plant for a year or two. As soon as the stools are built, they become the habitat of a number of plants such as *Bidens cernua*, *Polygonum hydropiperoides*, *Cyperus strigosus*, *Impatiens biflora*, *Peltandra virginica*, and others. These with *Decodon* and *Typha* seem, however, unable to persist, for dead stems of *Typha* and remains of stools of *Decodon* may be seen in

the cranberry-sphagnum association immediately behind this border vegetation. The last stage of a former large water area now occupied by the advancing cranberry-sphagnum association is shown in fig. 6. Cranberry and sphagnum build a mat and tufts of great compactness and gradually overcome and eliminate the swamp loosestrife (*Decodon*), cat-tail (*Typha*), *Peltandra*, and others. The advance of the mat out over the surface, even of open water, can be demonstrated by a series of such stages and

FIG. 7.—A sunken mat in the process of rejuvenation; the increased load upon the surface of the mat, especially after the heavier tree association became established, caused the sinking of the mat; the cutting of the timber reestablished equilibrium.

"last vestiges" indicating the existence of concentric zones of *Decodon* and *Typha* in quaking mats where formerly water occupied the area (fig. 4). The mats are floating, for test borings through them end abruptly in water which is quite free from fibrous material. The space of open water between the upper mat and the rest of the deposit below has frequently a depth of 4–5 feet (1.2–1.5 m.). In several places the peat below such mats is fine grained and well decomposed, not at all of a character that would indicate a transition structure from the coarsely fibrous to the well disintegrated, slightly fibrous deposit resting on the coarser mat below.

The sphagnum-cranberry formation is not to be regarded as an intercalation (18). The organic matter deposited by past generations of plants shows that sphagnums, cranberry, and their associates occupied this surface long before the maple-alder zone was formed. It is therefore an earlier and normal stage of succession, under conditions of development and a combination of factors which favored persistence and succession in that direction, and which are not suitable even today for the ecesis of a shrub-formation or for germination and growth of the seeds blown over in great quantities from the woodlots and fields surrounding the lake.

The vegetation in the central zone agrees very largely with plant societies in bogs and swamps of more northern regions. Many other "boreal" plants which were no doubt concerned in the early developmental stages of the local bog are now extinct. This is especially true of the pitcher plant (*Sarracenia purpurea*), the creeping snowberry (*Chiogenes hispidula*), wild rosemary (*Andromeda polifolia*), leather leaf (*Chamaedaphne calyculata*), labrador tea (*Ledum groenlandicum*), pale laurel (*Kalmia polifolia*), and larix (*Larix laricina*). The plants are still found in Ohio bogs north of here. A number of them have been recently transplanted and are now on the island in good condition.

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A MORPHOLOGICAL STUDY OF DIOSPYROS VIRGINIANA

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 145

STELLA M. HAGUE

(WITH PLATES I–III)

Diospyros virginiana, the northernmost representative of the tropical family Ebenaceae, grows abundantly in the southern states and as far north as the southern part of Illinois and Indiana. Cultivated trees are found also in the extreme northern part of those states. No report of any morphological work upon this family has been found, except a brief paper on "The seedless persimmon" in the report of the Proceedings of the Indiana Academy of Science for 1908. The material for this investigation was collected in 1906 and 1908 from cultivated trees at Decatur (Illinois), and from native trees near Springfield (Missouri), Topeka (Kansas), and Memphis (Tennessee).

Floral development

The winter buds are composed of numerous tough hairy scales enveloping a very rudimentary shoot. The flower buds develop upon this shoot during its rapid growth in the spring. At Decatur, in 1906, the buds began to swell and to become green the latter part of April. Young shoots gathered the first week in May bore flower buds in the early stages of development. On May 30 the shoots were 20 cm. or more long and the flowers were beginning to open.

So far as the trees from which material was collected were observed, they were dioecious and bore only imperfect flowers. One possible exception has been found recently. Near Auburn (Indiana) there is a cluster of staminate trees, originating apparently from one tree, that are reported to have borne fruit occasionally. The flowers were carefully examined in the spring of 1910, and no variations from the regular staminate type were found. Unless a pistillate tree has been cut away, it seems prob-

able that perfect flowers are borne some seasons, as has been reported from Kansas.[1]

The staminate flowers are smaller than the pistillate and in clusters (fig. 1), 16 fertile stamens surrounding the sterile pistil. The pistillate flowers are solitary, and usually contain 8 sterile stamens, but very often the number is greater.

The early stages of the development of the two flowers are the same. The floral cycles are generally preceded by a pair of bracts, though often there is only one (fig. 2). The calyx next appears (fig. 3) and becomes a massive enveloping cup before the other cycles can be seen, which appear in centripetal sequence (fig. 4). The corolla can be distinguished before the stamens, but they develop together in the typical sympetalous fashion. Occasionally the calyx or corolla has more than four parts; this is illustrated in fig. 6, in which the calyx has five divisions.

The stamens of the staminate flower fork (fig. 5), thus doubling the pistillate number (fig. 6); in the pistillate flower it is a common occurrence to find the number increased by the branching of one or more of the stamens. The fertile pistil contains eight ovules. The style is single, but the stigma is four-parted. Not many sterile pistils were examined; those that were had no ovules and a short imperfect style.

Megasporangium and megaspores

The ovule is anatropous and has two integuments (fig. 7), this last character being unusual among the Sympetalae. The mother cell can be distinguished by its size and conspicuous nucleus about the time the inner integument is first visible (fig. 8). Judging by the repeated appearance of this stage in the material, it is especially persistent. Only one mother cell occurs in a sporangium, and is always next to the outer layer of nucellar cells, no parietal cell being cut off. One complete figure of the first division of the mother cell was found in the spindle stage (fig. 9). Compared with the preceding conspicuous nucleus of the mother cell, the spindle is small and has very small and numerous chromosomes.

[1] The Industrialist, Kansas State Agricultural College, March 1904.

A portion of another figure showing the formation of the wall between the daughter cells was seen.

Four megaspores are formed in a linear row (figs. 10, 11), but it is not always complete, three cells not being uncommon. One exception to the usual arrangement was discovered, in which the outer daughter cell is divided by a vertical wall (fig. 12). As usual, the chalazal megaspore becomes the embryo sac (fig. 13).

Early stages of the embryo sac

The two and four-celled stages of the embryo sac were not found. At the eight-celled stage the sac is small, much longer than wide, and somewhat pointed at the micropylar end. When the sac is seen enveloped by the single nucellar layer, it appears decidedly cone-shaped, and is supported upon a stalklike portion of the nucellus as upon a pedestal (fig. 15). The growth of the sac does not obliterate this nucellar tissue until a comparatively late stage of the ovule. In the sac of fig. 14, which is the eight-celled stage in which the polars are differentiated, only seven nuclei are shown, and it seems quite probable that that is the full number for that particular sac, because there is much evidence that the usual number of nuclei is not always present. This conclusion is reached because of the conspicuous absence of antipodals. Three antipodals were found in one sac, but only after a long search. Extremely early disintegration would also account for the absence of these cells, but no evidence was found for this explanation.

The egg apparatus in the eight-celled stage shows nothing unusual. The three cells are in the ordinary position, and there is the customary differentiation of the cells in size.

In striking contrast to these two groups, the antipodals and egg apparatus, are the polars, which are large and conspicuous (figs. 21*a*, 21*b*), and are found either approaching or fusing in material gathered during the flowering time.

During the development of the sac the integuments become massive, and the innermost layer of cells of the inner integument becomes large and full of protoplasm, forming a tapetal layer com-

pletely enveloping the sac and extending around the stalklike nucellus and far up the micropyle (fig. 16).

The study of the sac is made difficult by the dense outer integument, through which killing fluids penetrate with difficulty, and also by the presence of chemicals which interfere with the stains. This last difficulty is especially true of the micropylar end of the sac, which when mature becomes a beaklike accumulation of a mucilaginous substance.

Pollination and fertilization

These studies have so far revealed only doubtful evidence of pollination and none at all of fertilization. Careful search has failed to show pollen tubes in the tissue of the style. The most positive evidence has been a few cases in which the mucilaginous substance has been divided in such a manner as to suggest a pollen tube penetrating the sac, and a few others in which there is the appearance of a swollen tip of a pollen tube within the sac. This evidence is discredited because the mucilaginous substance has been seen similarly divided too early for pollination, and the resemblance to the swollen tip of a pollen tube may be due to an incomplete or imperfect section of the stage shown in figs. 17*a* and 17*b*. Other slight evidence may be found in the presence of the spindle and chromosome-like bodies of figs. 19 and 20*b*. These may possibly have entered the sac by way of the pollen tubes or may have originated from the nuclei of the tube. The fusing polars which are so conspicuous have been carefully examined for a third nucleus but none has been seen.

The doubtful character of this evidence has naturally raised the question, whether pollination is essential to fruit and seed production. The field observations relating to pollination are limited and not very exact, but they suggest the possibility of an interesting problem. A tree in Decatur, from which material was collected in 1906, bears seeded fruit abundantly, though no staminate tree is known to be nearer than two miles. In order to see if the pollen was carried that distance or was essential, a branch was covered in the spring of 1909 during flowering time so as to prevent the

access of the bees. No fruit was borne on this branch, but was developed upon the neighboring ones. The details of this experiment cannot be vouched for, but until more careful ones are tried it is affirmative evidence for pollination.

On a fruit farm beyond the city limits of Decatur is a cluster of 6 or 8 trees, the largest of which is the parent of the smaller ones. The gardener reports that seedless fruit occurs on all these trees, but not in the same proportion. The fruit of the largest tree is usually many-seeded and only rarely seedless, but some of the smaller trees bear few-seeded and seedless fruit abundantly. No differences were noted among the flowers of these trees, or any when the prepared material was compared with that from native trees. The later stages are yet to be examined, for no collections have been made from the cluster after the flowering time.

The nearest staminate tree is not known. One was reported within a quarter of a mile, but two careful examinations of the region have failed to locate it. Since persimmon trees in bloom always swarm with bees, they are doubtless the pollinating agent. It does not seem probable that the bees avoid certain trees, but it is possible that the supply of pollen which they carry is limited, and is deposited most freely on those trees which from their position they visit first. The trees of the cluster which bear the larger proportion of abnormal fruit are the least exposed trees.

That the distance of the staminate trees does make a difference in the fruit is reported in the 1907 Yearbook of the Department of Agriculture, in which one variety is mentioned as characteristically few-seeded, and the observation made that this and other varieties have fewer seeds when grown at a distance from staminate trees.

In 1910 the Decatur trees were again visited. A severe frost in May killed the first buds, consequently the conditions that season were not normal. The city trees bore no fruit at all, and the cluster only a small proportion of its normal amount. The fruit on all the trees was smaller than usual, inclined to early decay, and almost wholly seedless. One lot of 33 contained only one seeded fruit; another of 12, two. The embryos were normal. This state of affairs suggests an indifference to fertilization, even

to pollination, as the stimulating cause of the development of the ovary into the characteristic persimmon fruit.

In the paper previously referred to on "The seedless persimmon," the seedless fruit is reported to occur most abundantly on the lowest branches of the trees. No differences were found in the flowers; all had a fertile pistil and sterile stamens. The examination of the embryo sacs brought out no evidence of pollination or fertilization. In one case cited, if pollen is transferred from the staminate trees, the bees must carry it three or four miles; this was not determined. Perfect flowers are suggested as a possible source of the pollen. Any attempt to explain or to suggest the problems of pollination involved is impossible until further observations are made.

Late stages of embryo sac; endosperm and embryo

The absence of evidence of pollination and fertilization has made impossible at present a connected account of the series of events in a normal seed-producing sac following the eight-celled stage, nor can these stages be surely identified, because the ovules of the seeded fruit frequently fail to develop into seeds, and since the normal course has not been determined, it is uncertain where the two diverge and what the differences are.

The entire ovule increases very rapidly in size after the corolla falls off, but no sign of an embryo was found for a number of weeks afterward. Material sent from Memphis is past blooming the latter part of May, but not until the last of June or the first of July can embryos be found easily in the fresh material. Long before this the sac has become densely filled with endosperm. Judging from the size of the sac, the first division of the primary endosperm nucleus follows closely on the fusion of the polars, and the other divisions follow rapidly after this (figs. 22, 23*a*, 23*b*).

The antipodal nuclei disappear after the eight-celled stage, but the micropylar nuclei undergo interesting changes. In fig. 17*a* there are three protoplasmic masses very distinctly differentiated. The middle one contains numerous, rather large, spherical, densely staining bodies. Because of its size, position, and

persistence in older sacs, this mass is surely the egg and the two other masses the synergids. Fig. 17*b* is another view of the same sac and shows the synergids more distinctly. Fig. 16 undoubtedly shows the two synergids, but no division of the surrounding protoplasm. In fig. 18 the egg appears with the spherical bodies regularly arranged; the small nucleus is a synergid. Fig. 19 is the micropylar end of a sac in which figures of dividing endosperm nuclei were seen. The large cell is the egg, near which are the spindle-shaped figures mentioned before. From their position it is possible that they are the remains of the disintegrating synergids. The large cell of fig. 24 is the egg at a later stage than the other figures show, because it is almost completely enveloped by the endosperm; numerous illustrations of this stage were found. No more distinct segmentation of the egg was seen than appears in fig. 25, in which the protoplasm is divided, but only one nucleus could be found, which makes it a doubtful case. Even after the egg is completely surrounded by endosperm, the deeply staining globules remain, but they and the whole egg seem to lose the prominence shown in fig. 24. However, this is partly relative owing to the increased size of the whole ovule. Figs. 20*a* and 20*b* show the curious chromosome-like bodies in the micropylar end of the sac; they are rodlike and twisted, resembling chromosomes, but not those of *Diospyros*, which are very small. The investigation of these phases of the life history of the persimmon will be continued in the hope that the complete sequence of events in the embryo formation will be found.

The youngest unmistakable embryo that has been seen consists of three cells (fig. 26). This embryo was in the extreme micropylar end of the sac, imbedded in endosperm. Its position agreed very nearly with that of the egg when surrounded by endosperm, but no proof could be found that it originated from that cell. Fig. 27 represents the embryo at a much later stage, but does not yet show differentiation into stem tip and cotyledons. Fig. 28 is a variation from the common type, and fig. 29 is the appearance of the embryo about the time it can be distinguished without a lens. One case of polyembryony was found (fig. 30), and one lot of material contained freak embryos, one of which is shown in

fig. 31, in which a second pair of cotyledons has developed upon one of the original pair.

Microsporangium and pollen

The studies of the stamens and pollen were made from material collected in 1906 from a single tree near Decatur. This tree bloomed a few days later than the pistillate trees from which collections were being made at the same time. The pollen formation was easily traced. The only difficulty encountered was in the late stages when the protoplasm is dense and evidently contains the same chemicals that interfere with the stains in the embryo sac.

Each stamen produces four sporangia, whose early stages were not traced because the earliest collections were made May 28, about a week before the flowers opened. At that date the sporangia contained large pollen mother cells surrounded by a single tapetal layer (fig. 33). The division into tetrads is shown in figs. 34 and 35. The figures are small and the chromosomes numerous, 30 at least. In the mature pollen grain more than one nucleus could be rarely distinguished, and that one not nearly so conspicuous as the nucleus of the tetrad (figs. 36, 37). It is very possible that the dense protoplasm frequently obscures the second small nucleus. A considerable difference in the size of the pollen grains was noted; this and the frequent presence of a single nucleus, together with the lack of proof of pollination, raise the question of the fertility of the pollen. This remains to be determined along with the other problems of pollination.

Summary

1. The flowers are developed on shoots of the same season's growth. The floral cycles appear in the following order: a pair of bracts, the calyx, the corolla and stamens, and lastly the pistil.

2. The ovule is anatropous and has two integuments. A single mother cell is formed beneath the outermost layer of the nucellus, from which four megaspores develop, the chalazal one becoming the embryo sac.

3. The embryo sac at the eight-celled stage is small, somewhat pointed at the micropylar end, and rests upon a stalklike portion of the nucellus. A tapetal layer of cells from the inner integument completely surrounds it. The egg apparatus in this stage is not conspicuous; the polars are large and striking in appearance; the antipodals are found with so much difficulty that it is probable that one or more of the cells is often lacking.

4. The studies of pollination and fertilization are not complete. Little evidence of pollination has been found and none of fertilization. The production of seedless fruit is probably involved in the problem of pollination.

5. After the flowers fall, the whole ovule increases rapidly in size. The egg enlarges and becomes filled with densely staining globules. The primary endosperm nucleus divides early and the endosperm fills the sac, and then crowds the inner integument quite up to the dense outer one.

6. The embryo is late in appearing. The earliest stage identified was a three-celled one in the extreme micropylar region. The tendency to variation seen in many of the stages is shown here in the two types found, the freak embryos and the case of polyembryony.

7. Pollen mother cells were found on a tree a week before the older flowers opened. The mother cells are large and the whole mass is surrounded by a single tapetal layer. The spindle in the tetrad formation is small, the chromosomes being 30 or more. The pollen grains show some difference in size, and frequently only one nucleus could be distinguished.

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AUBURN, IND.

EXPLANATION OF PLATES I–III

FIG. 1.—Diagram of a cluster of staminate buds.

FIG. 2.—A pistillate bud, showing enveloping bracts (*b*).

FIG. 3.—A pistillate bud, showing a single bract (*b*) and the beginning of the calyx.

FIG. 4.—A pistillate bud, showing calyx (*k*), corolla (*c*), stamens (*s*), and pistil (*p*).

FIG. 5.—A staminate flower, showing calyx (*k*), corolla (*c*), the two stamens (*s*), and pistil (*p*).

FIG. 6.—A cross-section of a pistillate flower, showing the unusual division of the calyx into five parts, the union of the corolla, and the four parts of the pistil; diagram.

FIG. 7.—An ovule with the two integuments.

FIG. 8.—The nucellus containing the mother cell, and showing the beginning of the inner integument (*i*).

FIG. 9.—First division of the megaspore mother cell.

FIG. 10.—The two daughter cells.

FIG. 11.—The four megaspores.

FIG. 12.—The four megaspores; the outer daughter cell divided by a vertical wall.

FIG. 13.—The functioning megaspore; the others disintegrating.

FIG. 14.—Embryo sac; polars differentiated.

FIG. 15.—Diagram of an ovule showing the relative size of the parts, the shape of the sac (*e*), the stalklike nucellus (*n*), and the massive integuments (*i*).

FIG. 16.—The micropylar end of the embryo sac, showing the synergids and the enveloping tapetal layer.

FIG. 17*a*.—Micropylar end of sac; synergids and egg.

FIG. 17*b*.—Same sac as 17*a*, showing fusing polars.

FIG. 18.—Micropylar end of sac; one synergid and the egg.

FIG. 19.—Micropylar end of sac; egg and spindle-shaped bodies.

FIG. 20*a*.—A detail of the micropylar end of a sac, showing the chromosome-like bodies and the egg filled with the densely staining globules.

FIG. 20*b*.—Same as 20*a*; chromosome-like bodies more clearly shown.

FIG. 21*a*.—Fusing polars.

FIG. 21*b*.—Fusing polars.

FIG. 22.—First division of the primary endosperm nucleus.

FIG. 23*a*.—Division of endosperm nucleus.

FIG. 23*b*.—Division of endosperm nucleus.

FIG. 24.—Egg almost surrounded by endosperm.

FIG. 25.—Egg; segmentation suggested.

FIG. 26.—Young embryo.

FIG. 27.—Young embryo.

FIG. 28.—Variation of type of embryo.

FIG. 29.—Shape of embryo at the time it can be seen without a lens; diagram.

FIG. 30—Polyembryony; diagram.

FIG. 31.—A freak embryo; a second embryo (c^2) developing on one of the first pair of cotyledons (c^1); diagram.

FIG. 32.—Diagram of a cross-section of an anther, showing the four sporangia.

FIG. 33.—Pollen mother cells.

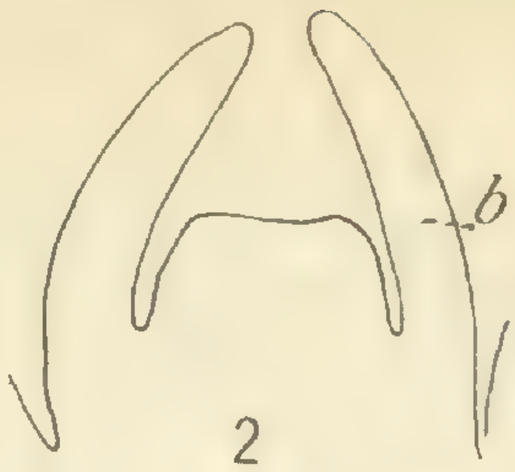
FIG. 34.—Formation of tetrads.

FIG. 35.—Tetrads.

FIG. 36.—Pollen grain; one nucleus.

FIG. 37.—Pollen grain; two nuclei.

1



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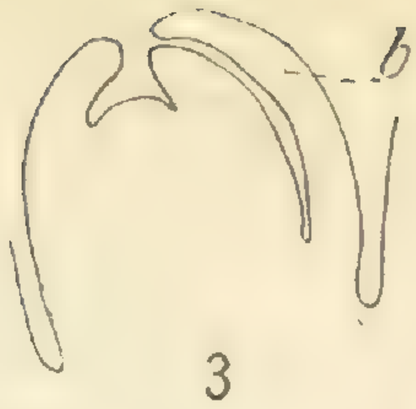

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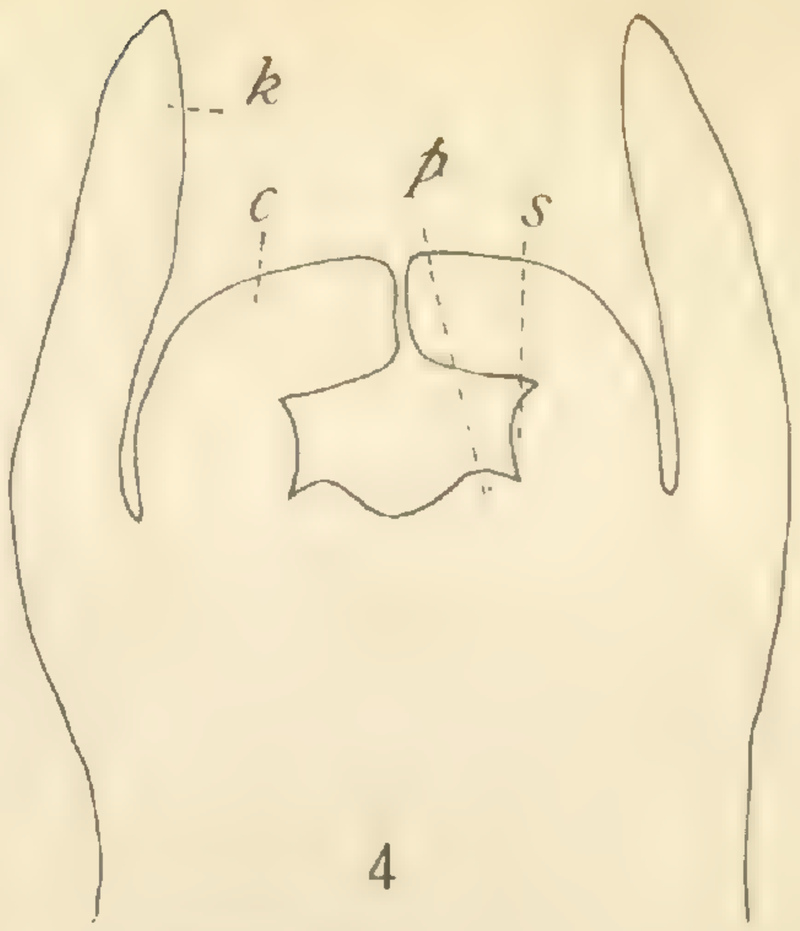

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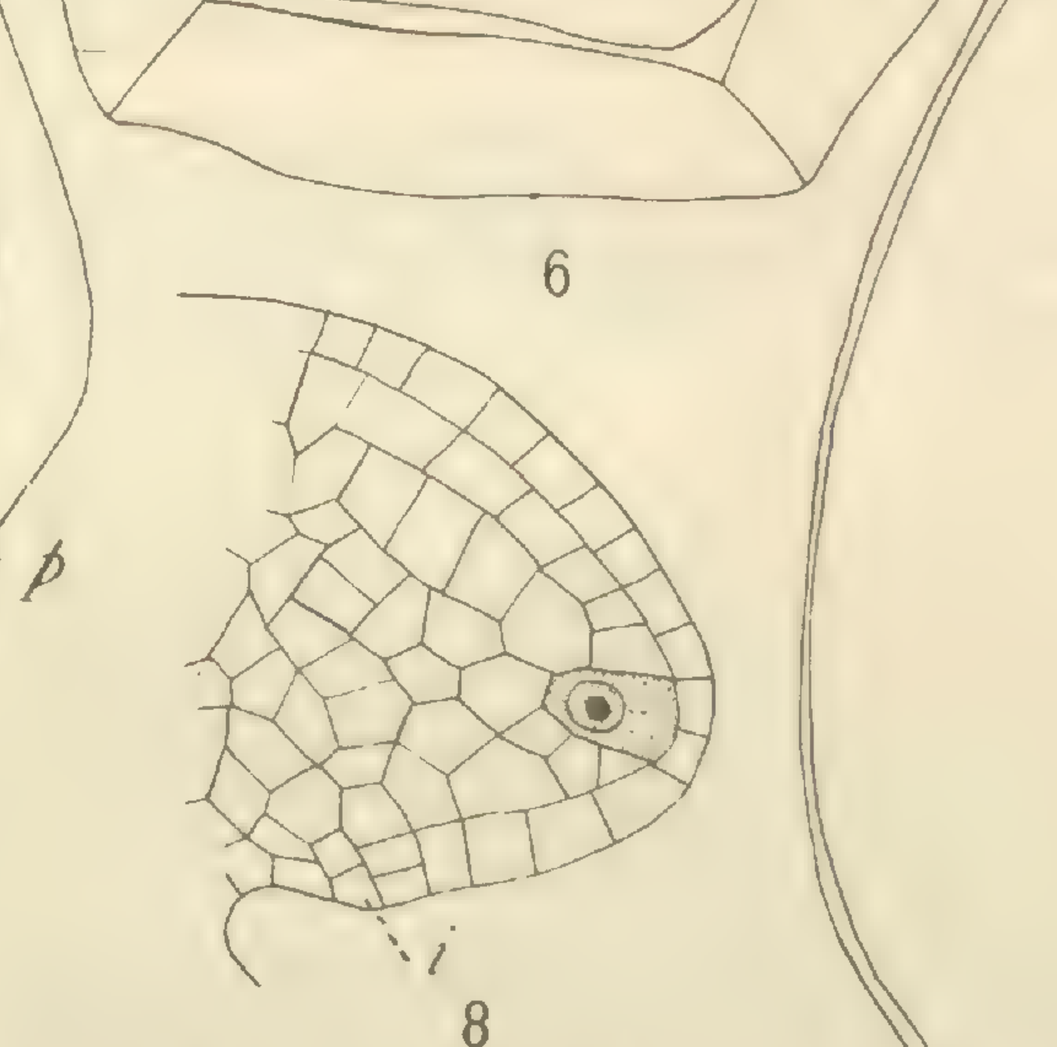

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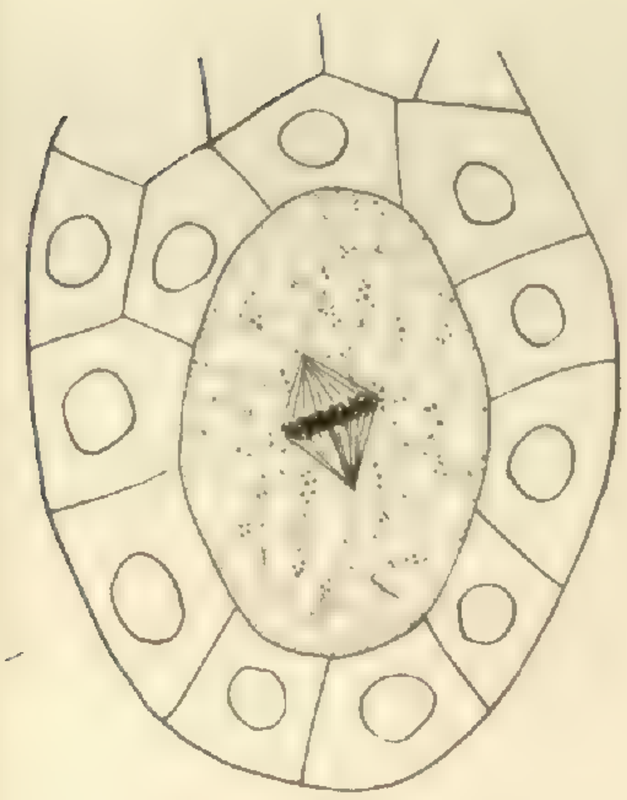

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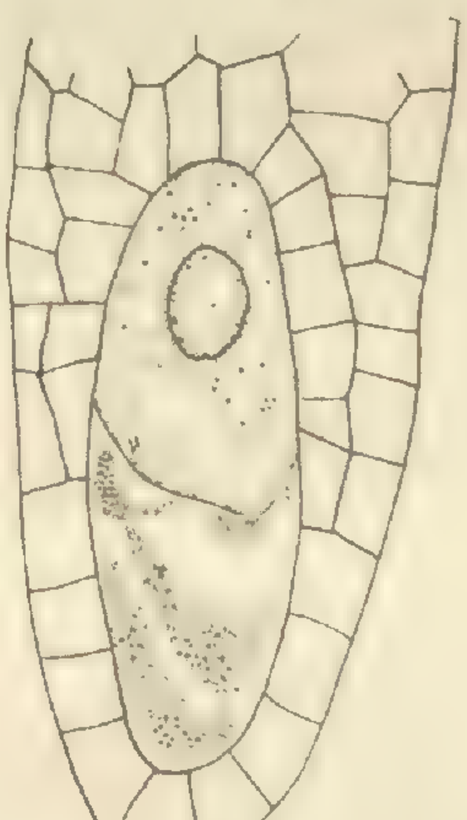

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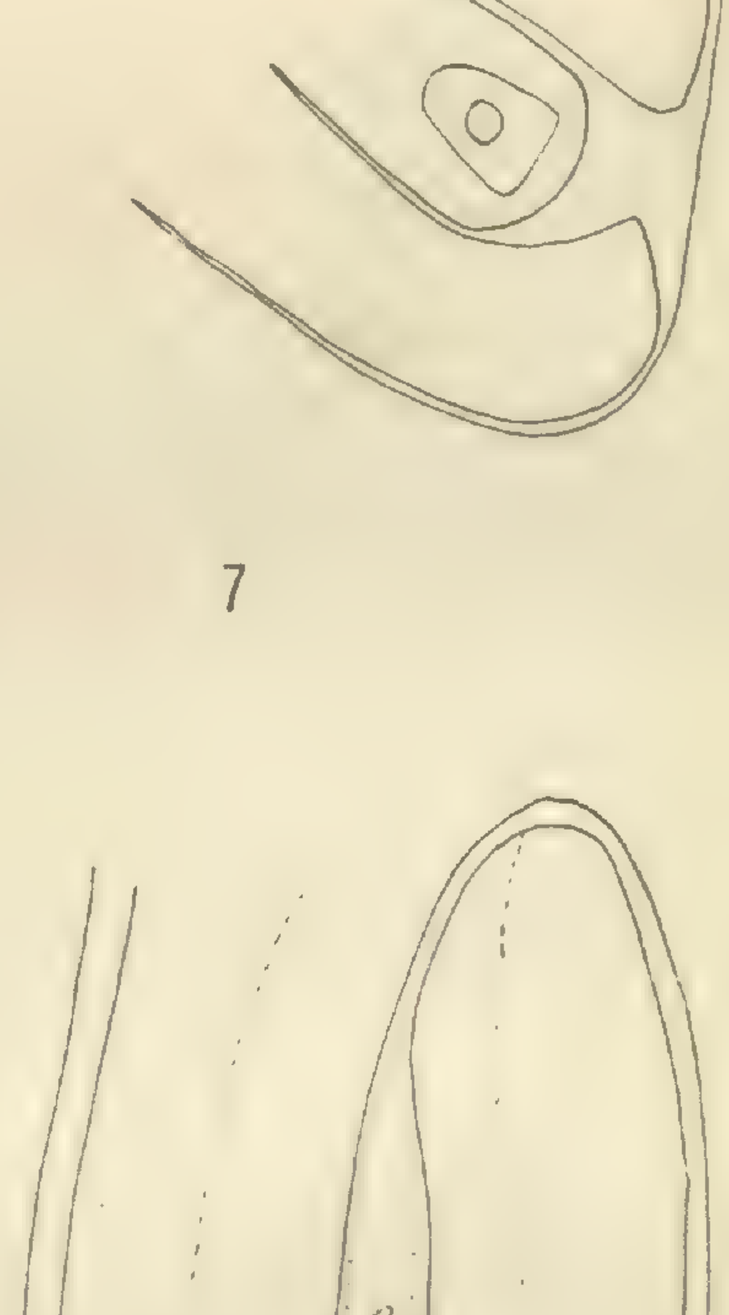

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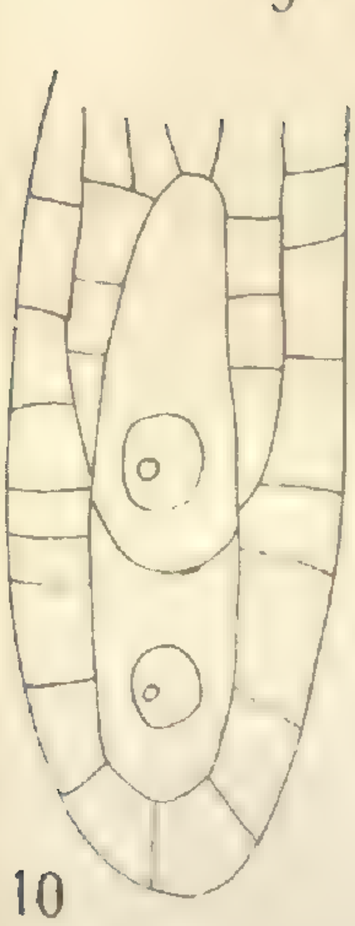

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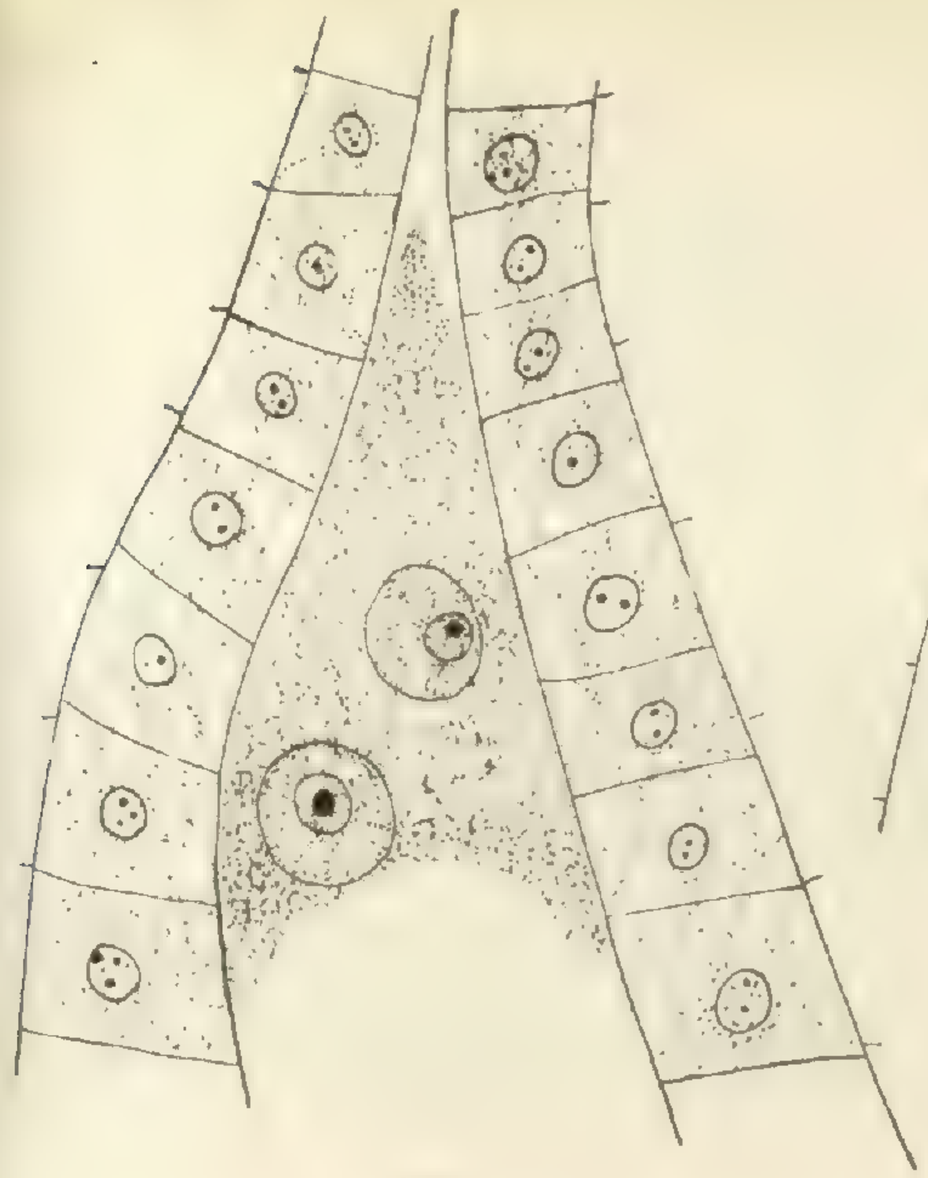
HAGUE on DIOSPYROS



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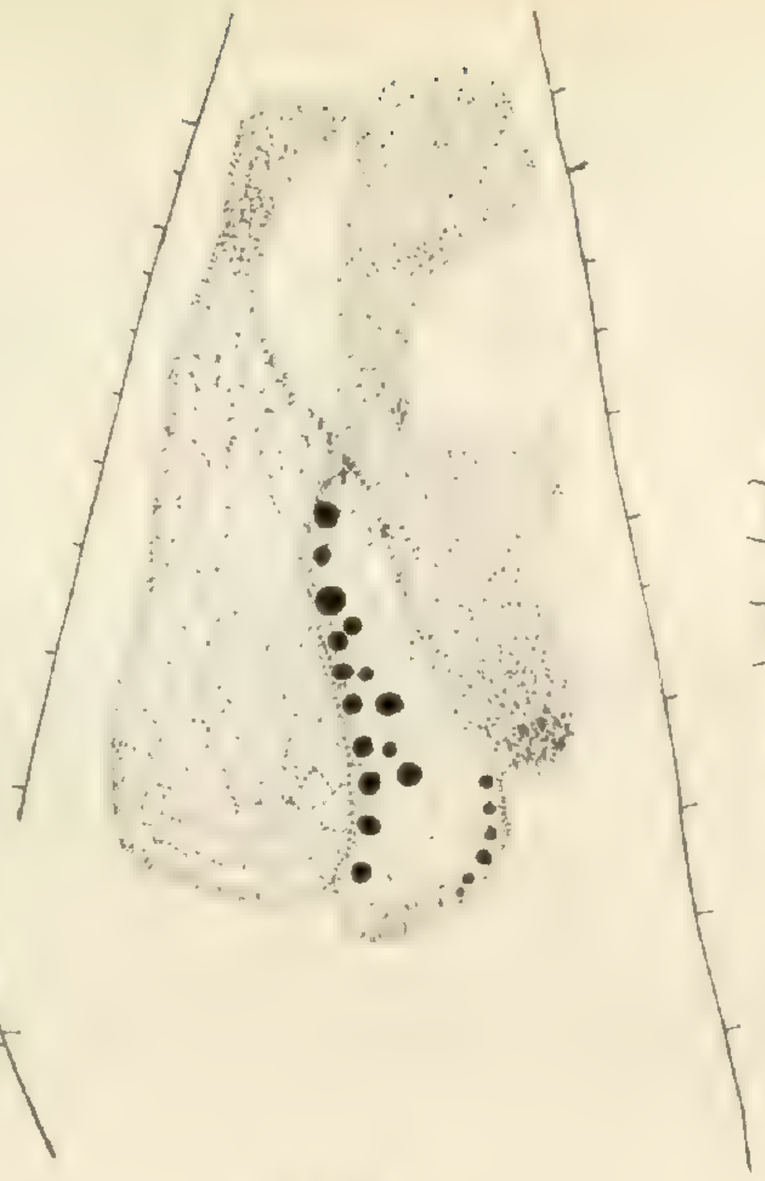

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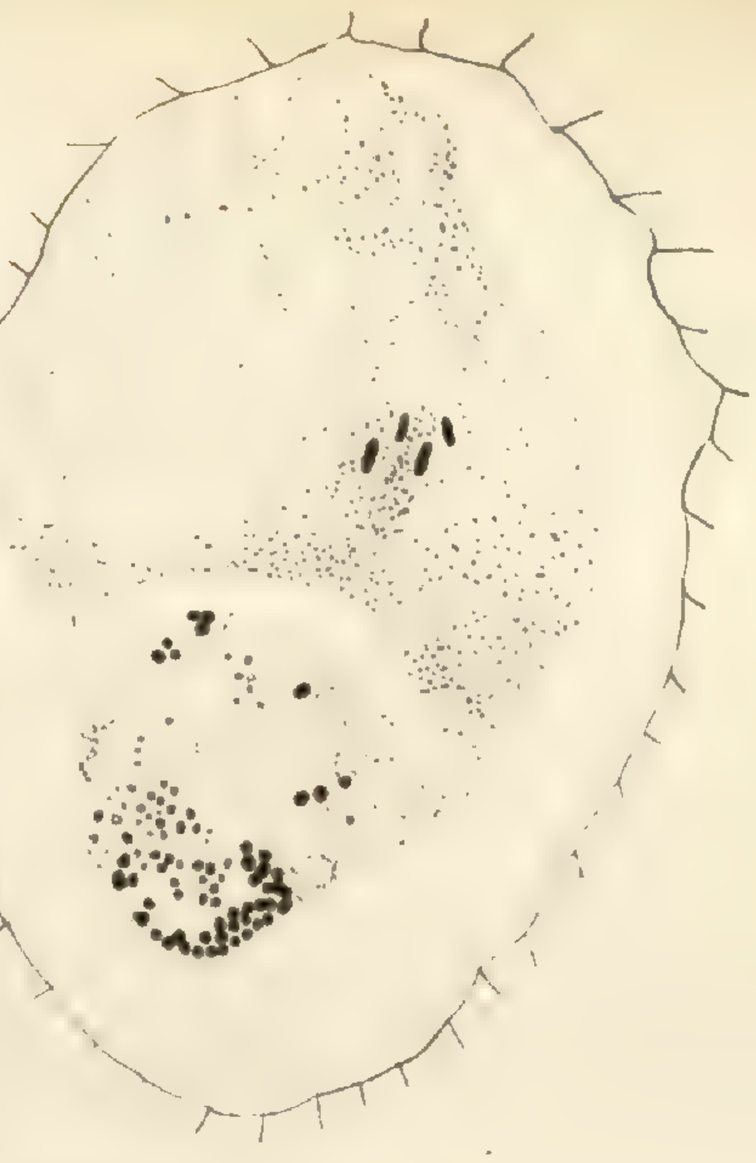

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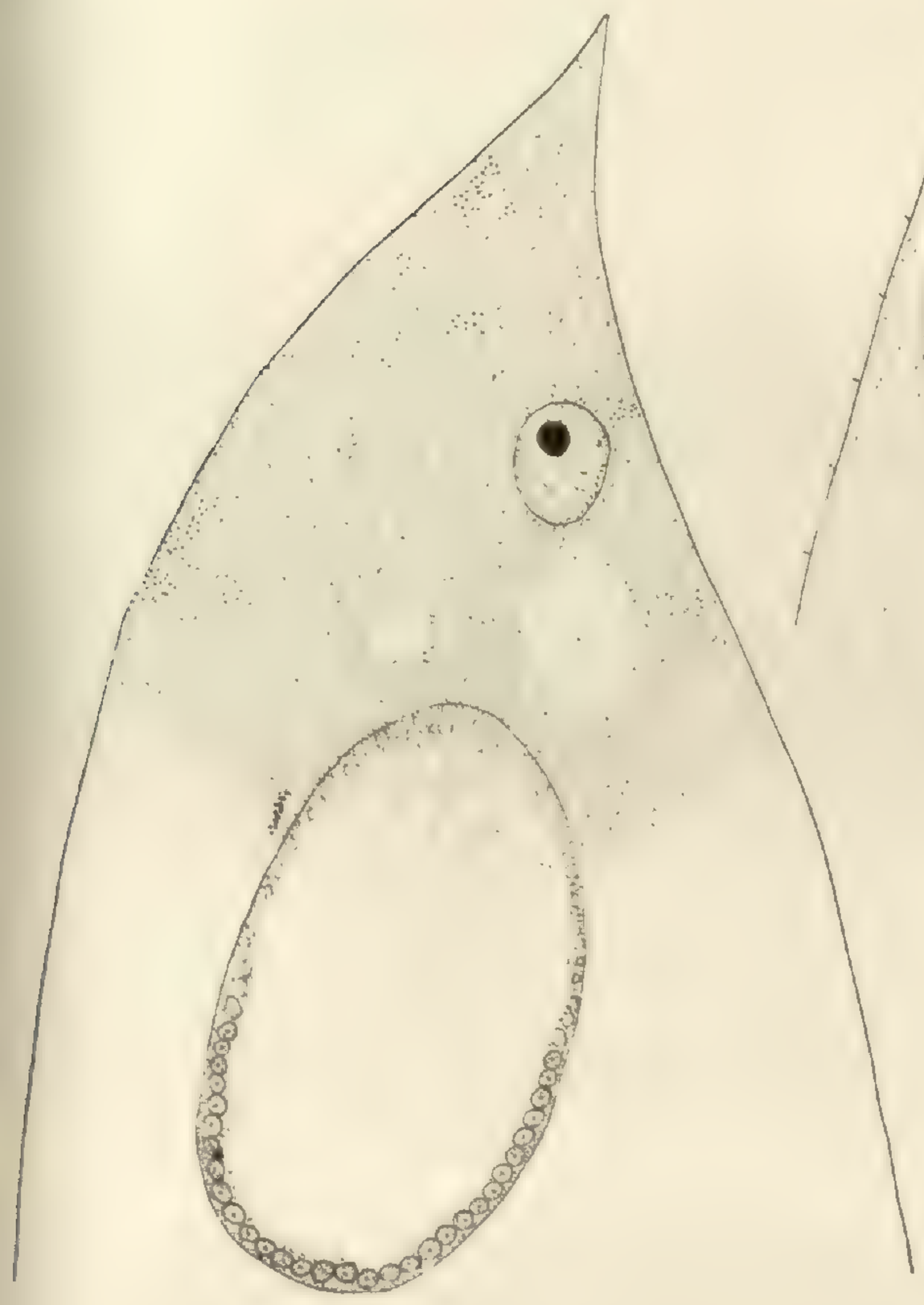

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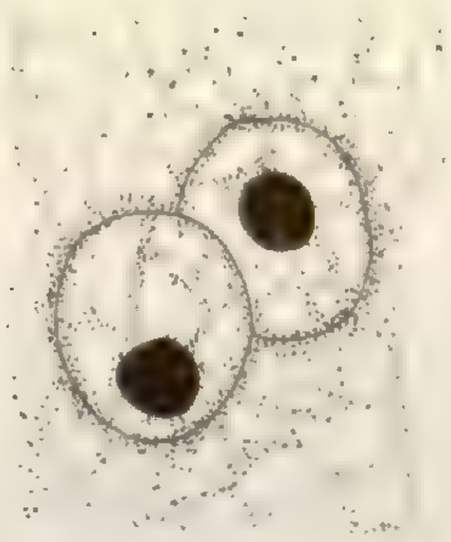

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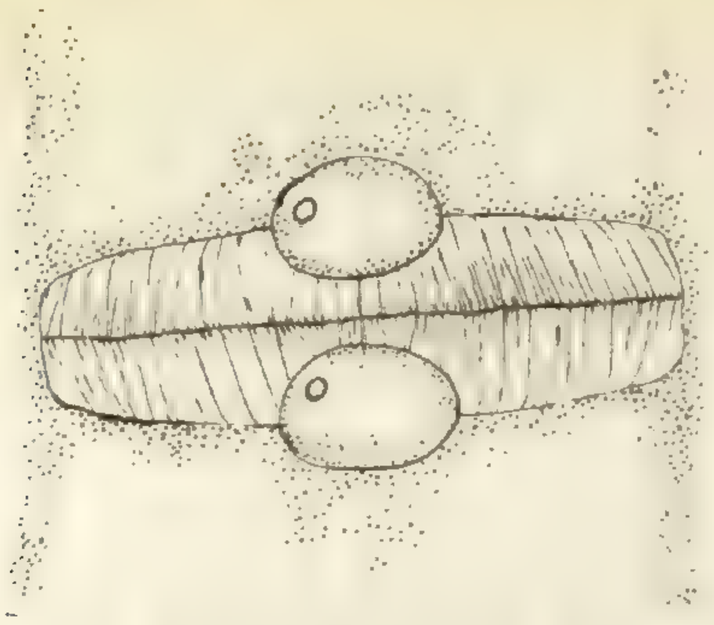

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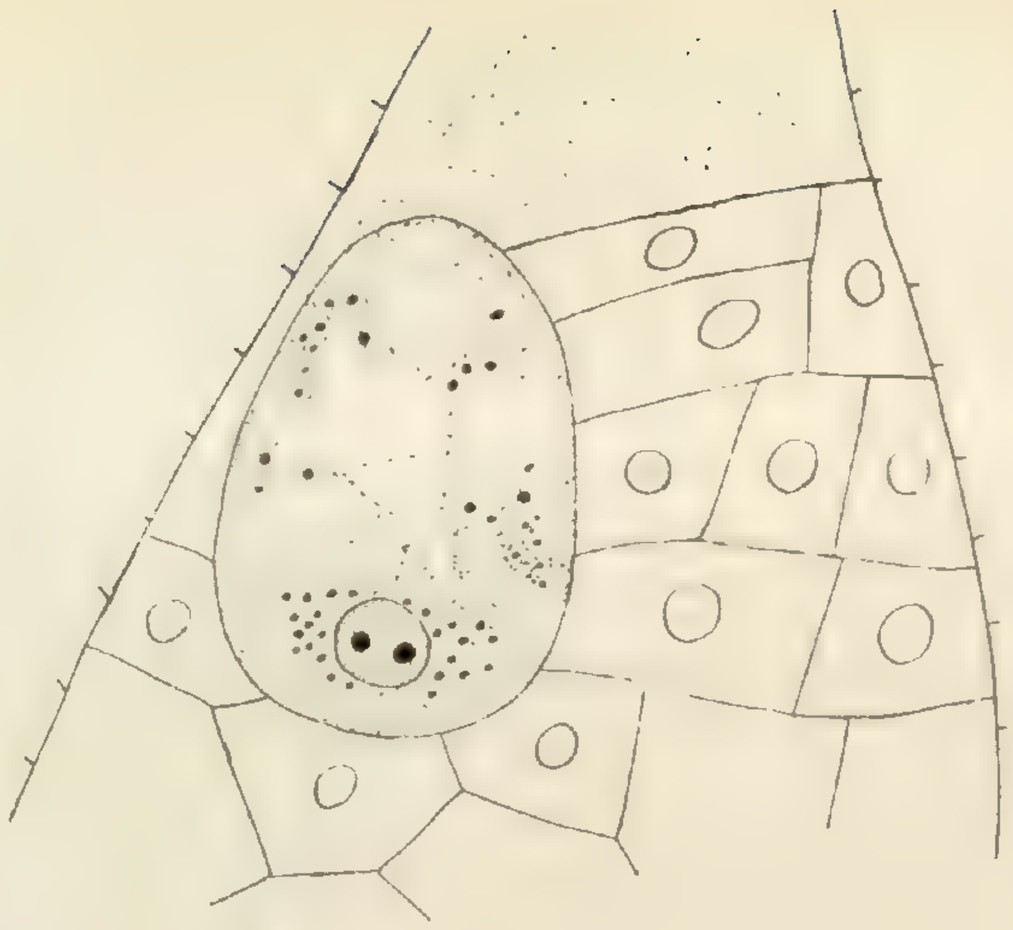

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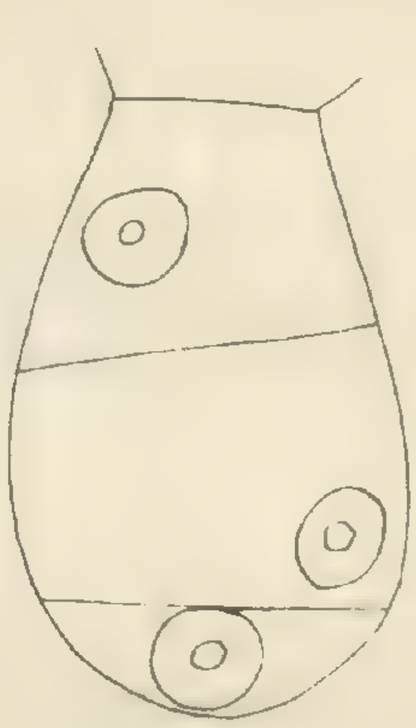

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C2

C1

C

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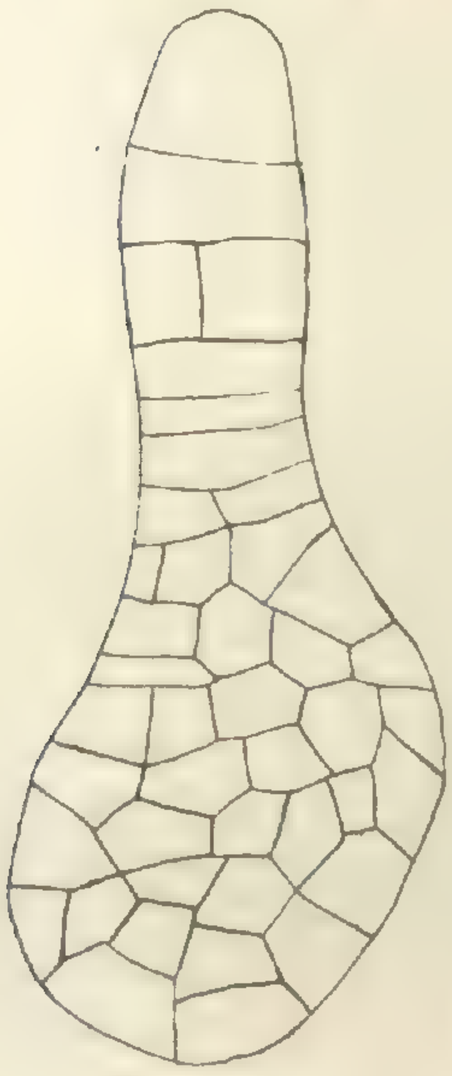

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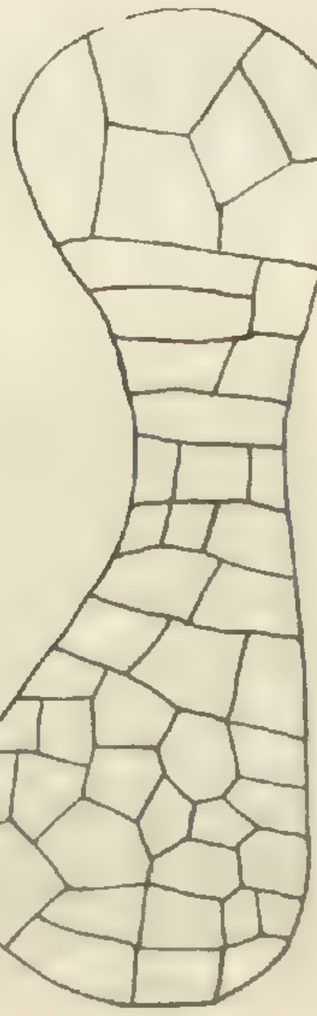

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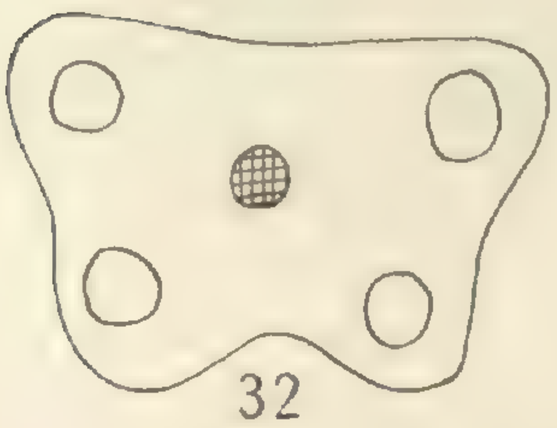

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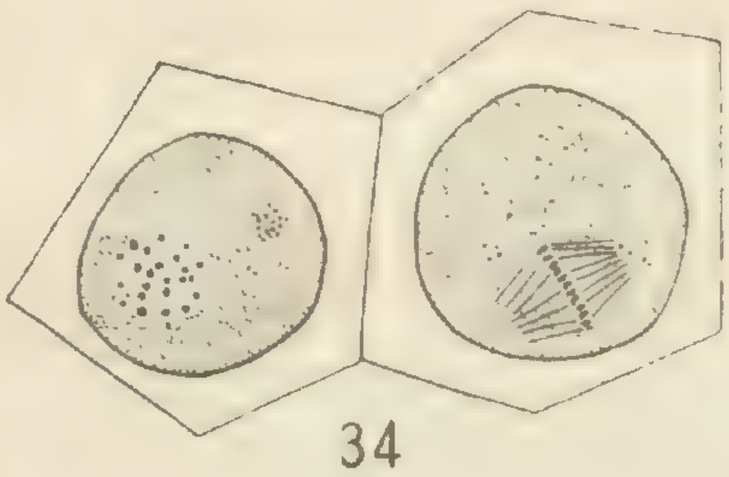

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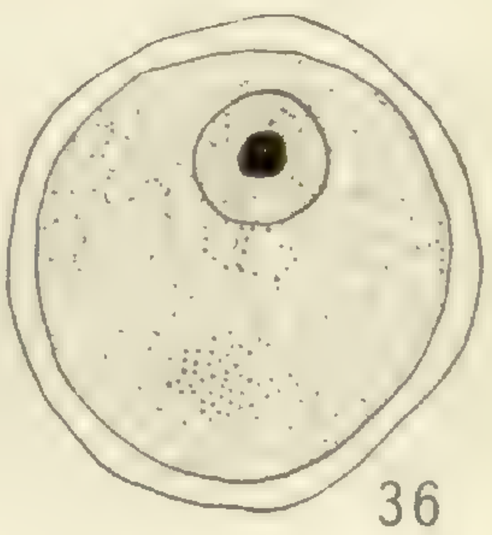

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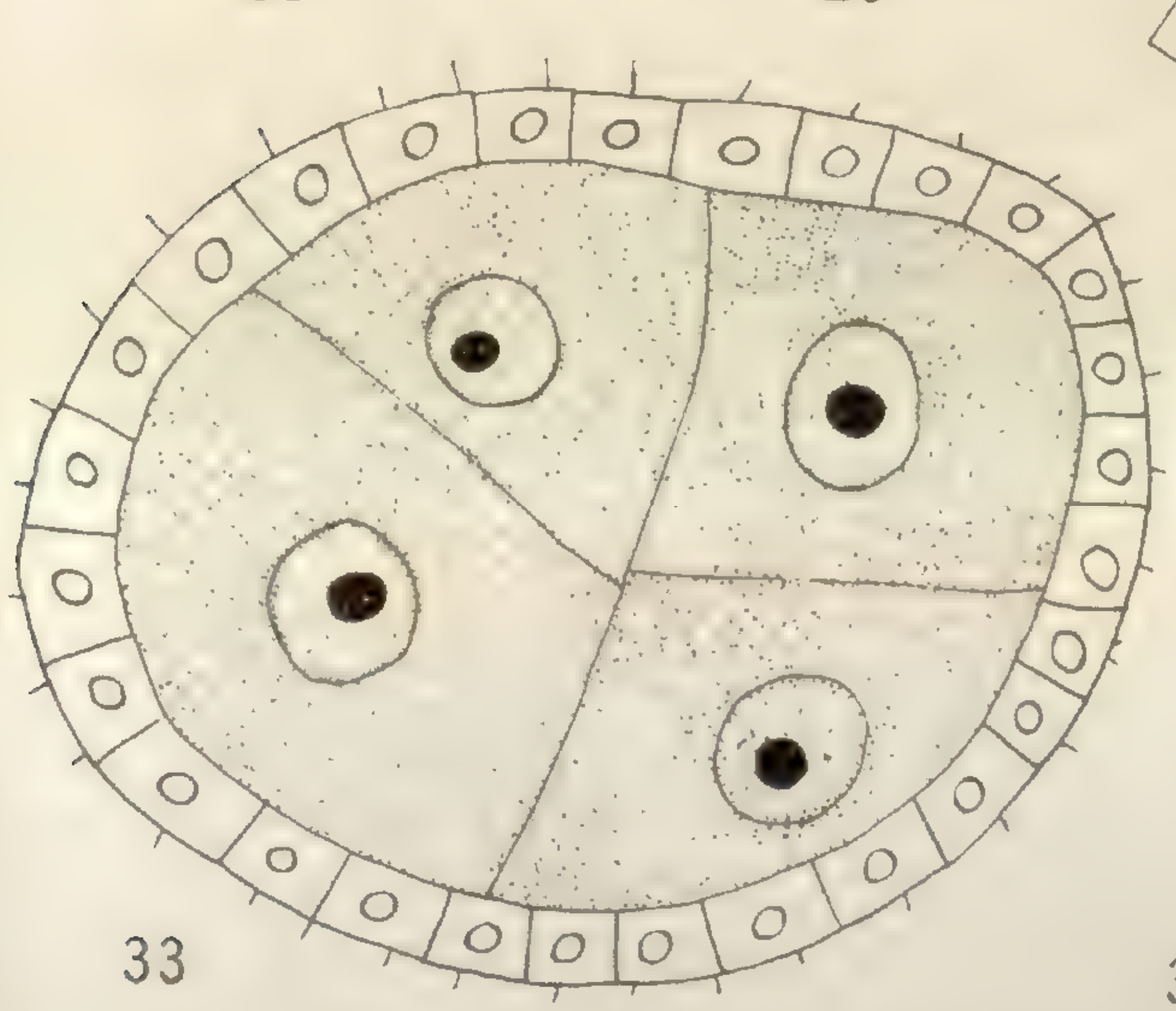

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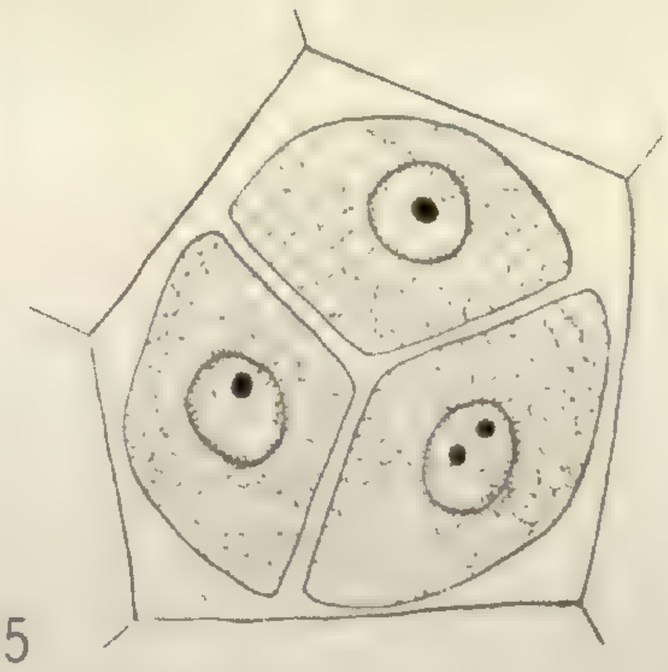

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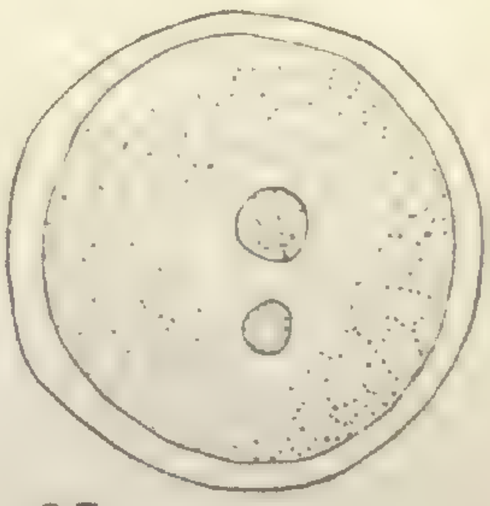


37

HAGUE on DIOSPYROS

UNDESCRIBED PLANTS FROM GUATEMALA AND OTHER CENTRAL AMERICAN REPUBLICS. XXXIV[1]

JOHN DONNELL SMITH

Thouinia brachybotrya Donn. Sm.—Folia petiolo parum longiora trifoliolata, foliolis ovato- vel obovato-ellipticis utrinque acutis crenulatis supra puberulis subtus velutinis. Racemi axillares singuli simplices tenues breves densiflori. Samara subsemicircularis, alae latere interiore axin centralem 3-plo superante, exteriore loculum marginante.

Arbor 5-metralis, ramulis novellis petiolis racemis canescentibus. Foliorum juvenilium tantum visorum petiolus 1–2.5 cm. longus, foliola 4–5 cm. longa 16–20 mm. lata pellucido-reticulata, nervis lateralibus utrinsecus 10–12 furcatis marginem attingentibus, petiolulis 1 mm. longis. Racemorum pedunculus 3–6 mm. longus, rhachis 15–22 mm. longa vix 1 mm. crassa, pedicelli e nodulo piloso squama transversim elliptica intus glabra cincto orti 3–4 mm. longi rubiginosi. Sepala 1.5 mm. longa intus glabra. Stamina 1.5 mm. longa, filamentis inferne pilosiusculis, antheris glabris. Ovarii cano-velutini lobi subrhomboidei 2.5 mm. longi apice obtusi axin centralem subaequantes stylum trifidum inferne cano-velutinum paulo superantes. Samara abortione saepe solitaria 20 mm. longa 10 mm. lata velutina tota flabellinervata, alae latere interiore recta, exteriore arcuata, axe centrali incana 5 mm. longa, loculo 6 mm. longo, semine ovali 4.5 mm. longo, testa ferruginea. Petala in exemplis suppetentibus deficientia.

Ad ripas fluminis *Río Grande* dicti, Depart. Zacapa, Guatemala, alt. 230 m., Jun. 1909, *Charles C. Deam*, n. 6343.

Calopogonium phaeophlebium Donn. Sm.—Foliola elliptico-oblonga utrinque obtusa vel obtusiuscula supra pilis appressis conspersa subtus praeter nervos primarios fulvescentes cano-sericea. Racemi pedunculati foliis longiores remote nodiferi, floribus 1–5-nis subsessilibus minimis. Calycis segmenta tubo paulo longiora. Vexillum calyce parum longius. Legumen fulvo-strigillosum gracillimum polyspermum.

Herba volubilis, caulibus petiolis racemis retrorsum fulvo-pilosis. Foliola membranacea discoloria 5.5–8.5 cm. longa 2–3 cm. lata mucronulata, lateralia

[1] Continued from BOT. GAZETTE 49:458. 1910.

paulo minora inaequilatera subsessilia, nervis lateralibus utrinque 7–8 rectis simplicibus marginem attingentibus subtus conspicuis, petiolo communi 3.5–6 cm. longo, petiolulo terminali 6–8 mm. longo, stipulis stipellisque minute setaceis. Racemi pedunculo 2–5 cm. longo computato 12–20 cm. longi, pedicellis vix 1 mm. longis, bracteolis minute setaceis, floribus 7 mm. longis. Calyx fulvo-strigillosus 5 mm. longus, segmentis setaceo-acuminatis, duobus summis usque ad medium connatis. Vexillum violaceum 6 mm. longum alis carinisque longius, lamina fere orbiculari 3 mm. lata exauriculata. Stamen vexillare omnino liberum. Ovarium sericeum, stylo ad medium sensim incrassato. Legumen (in exemplis suppetentibus nondum satis maturum) deflexum lineare 5 cm. longum 3 mm. latum rectum apice falcatum, seminibus circiter 8–10.—*C. racemoso* M. Micheli proximum, floribus tamen *C. galactioidem* Benth. revocantibus. Ad ripas Laguna de Ayarza, Depart. Jalapa, Guatemala, alt. 2440 m., Sept. 1892, *Heyde et Lux*, n. 3742 ex Pl. Guat. quas ed. Donn. Sm.—Cuajiniquilapa, Depart. Santa Rosa, Guatemala, alt. 910 m., Sept. 1893, *Heyde et Lux*, n. 6096 ex Pl. Guat. quas ed. Donn. Sm.—Secanquím, Depart. Alta Verapaz, Guatemala, alt. 570 m., Jan. 1905, *George P. Goll*, n. 226.—Río Torres, San Francisco de Guadalupe, Prov. San José, Costa Rica, alt. 1170 m., Nov. 1894, *Adolfo Tonduz*, n. 8968.

Exemplum Gollianum in herbario Musei Nationalis sub numero proprio 860576 servatur.

Hauya (§ SESSILIFLORAE) **microcerata** Donn. Sm. et Rose.—Folia longiuscule petiolata obovata vel oblongo-obovata supra glabrescentia subtus cinereo-tomentosa. Flores inter maximos. Calycis laciniae tubo bis et ultra superatae pro rata brevissime appendiculatae. Capsula dorso ecarinata.

Arbuscula e schedula Tuerckheimiana, ramulis novellis et alabastris appresso-canoque pubescentibus. Folia primum ovalia supra pilosiuscula, demum 7–11 cm. longa 4–6 cm. lata abrupte breviterque cuspidata basi acuta venulis pellucida, nervis lateralibus subrectis utrinsecus 7–9, petiolis gracilibus 3–4 cm. longis tomentulosis, stipulis incurvo-subulatis 2 mm. longis glabris nigris. Calycis pubescentis tubus 8.5–10 cm. longus, laciniae 3.5–4 cm. longae, appendicula 3–4 mm. longa cano-velutina. Petala ovalia 33 mm. longa 23 mm. lata. Antherae 18 mm. longae filamentis aequilongae. Ovarium patule cano-velutinum 11 mm. longum, stigmate elliptico 5 mm. longo supra petala vix exserto. Capsula 5 cm. longa, seminibus deficientibus.

Santa Rosa, Depart. Baja Verapaz, Guatemala, alt. 1500 m., Sept. 1888, *H. von Tuerckheim*, n. 1423 ex Pl. Guat. etc. quas ed. Donn. Sm. (Typus).—Cuesta di Quililhá prope Purulá, Depart. Baji Verapaz, Guatemala, alt. 1400 m., Apr. 1905, *H. Pittier*, n. 155.—Canjob, Prov. Chiapas, Mexico, alt. 1350 m., Maj. 1904, *E. A. Goldman*, n. 923.

Exempla nn. 155 et 923 in herb. Musei Nationalis servantur.

Hauya (§ SESSILIFLORAE) **quercetorum** Donn. Sm. et Rose.—Folia ex orbiculari-ovali ovata cuspidata vel saltem acuta basi rotundata vel emarginata supra glabra, costa nervisque subtus ciliatis vel glabrescentibus. Calycis laciniae tubo subdimidio breviores longe appendiculatae. Ovarium pubescens. Capsula inter minores.

E schedula repertorum arbor. Ramuli glabrescentes foliorum cicatricibus arcte notati, partibus novellis cano-hirsutis. Folia subtus plerumque glauca 6–12 cm. longa 5–6.5 cm. lata, nervis lateralibus utrinque 8–9, petiolis pilosis vel glabrescentibus 1.5–2.5 cm. longis, stipulis aristuliformibus vix 1 mm. longis puberulis. Calycis pubescentis vel glabri tubus 7–9 cm. longus, laciniae 3.5–5 cm. longae, appendicula 10–13 mm. longa pubescente vel glabra. Petala 3 cm. longa. Filamenta 24 mm. longa antheris dimidio longiora. Ovarium 10–11 mm. longum, stigmate ellipsoideo 5 mm. longo paulo exserto. Capsula 3.5 cm. longa, valvis dorso planis, seminibus lanceolatis 15 mm. longis 5 mm. latis acutis, ala basi involuta incrassata latere altero producta.

In quercetis ad declivitates montis *Jumaytepéque* dicti, Depart. Santa Rosa, Guatemala, alt. 1850 m., Mart. 1893, *Heyde et Lux*, n. 4479 ex Pl. Guat. etc. quas ed. Donn. Sm. (Typus); Dec. 1892, *Heyde et Lux*, n. 4336 ex Pl. Guat. etc. quas ed. Donn. Sm.

Hauya (§ SESSILIFLORAE) **ruacophila** Donn. Sm. et Rose.—Folia orbiculari-cordata vel basi rotundata ovalia cuspidata supra glabra subtus costa nervisque dense cano-ciliata ceterum pilis deciduis conspersa. Calycis laciniae tubo subdimidio breviores appendicula elongata cano-ciliatae. Ovarium velutinum. Capsula inter majores.

Arbor mediocris, ramulis novellis velutinis. Folia 5–7 cm. longa 3–6 cm. lata, nervis lateralibus late patulis arcuatis utrinsecus 7–8 et costa subtus conspicuis, petiolis 12–25 mm. longis hirsutis vel velutinis, stipulis aristiformibus 2 mm. longis pubescentibus. Calycis pubescentis tubus 9.5–10 cm. longus, laciniae 5–5.5 cm. longae appendicula 10–12 mm. longa instructae. Petala elliptica 4.5 cm. longa 2.5 cm. lata. Filamenta 25 mm. longa antheris subaequilonga. Ovarium 13–15 mm. longum, stigmate globoso 8 mm.-diametrali vix exserto. Capsula 6 cm. longa, valvis dorso planis, seminibus oblongis 13 mm. longis 4 mm. latis obtusis, ala basi involuta incrassata latere altero producta.

In silvis ad montem *Volcán Acatenango* dictum, Depart. Zacatepéquez, Guatemala, alt. 1700 m., Mart. 1892, *John Donnell Smith*, n. 2528 ex Pl. Guat. etc. quas ed. Donn. Sm. (Typus).—Alotenango in declivitatibus praeruptis montis *Volcán di Fuego* dicti, Depart. Zacatepéquez, Guatemala, alt. 1300 m., Mart. 1892, *John Donnell Smith*, n. 2527 ex Pl. Guat. etc. quas ed. Donn. Sm.

Hauya (§ SESSILIFLORAE) **lemnophila** Donn. Sm. et Rose.—Folia oblongo-ovata vel -elliptica vel -obovata cuspidata vel saltem acuta basi rotundata vel obtusa supra glabrescentia subtus hirsuta. Calycis laciniae tubo subtriente breviores, appendicula pro rata longissima. Filamenta antheris dimidio longiora. Ovarium hirsutum. Capsula maxima.

E schedula repertorum arbor. Ramuli foliorum subtus nervi petioli uti ovarium patule cinereo-hirsuti. Folia maxima subcoriacea circumscriptione summe variabilia, adulta plerumque oblongo-elliptica 9–15 cm. longa 4.5–7.5 cm. lata nonnunquam subtus glabrescentia, nervis lateralibus subrectis utrinsecus 7–9, petiolis 2.5–4 cm. longis, stipulis aristiformibus 2 mm. longis pubescentibus. Flores e schedula albi. Calycis tubus 7.5–9 cm. longus, laciniae 4.5–5 cm. longae, appendicula in alabastro 16–18 mm. longa in flore 12 mm. longa. Petala 33–35 mm. longa. Filamenta 20 mm. longa, antheris 13 mm. longis. Ovarium 13–14 mm. longum, stigmate vix exserto. Capsula linearioblonga 7.5–8 cm. longa, valvis dorso planis, seminibus deficientibus.

Ad ripas lacus *Carrizal* dicti, Depart. Santa Rosa, Guatemala, alt. 1360 m., Maj. 1892, *Heyde et Lux*, n. 2936 ex Pl. Guat. etc. quas ed. Donn. Sm.

Hauya (§ PEDUNCULATAE) **lucida** Donn. Sm. et Rose.—Praeter foliorum nervos subtus glabrescentes omnibus in partibus glaberrima. Folia nitida obovata vel elliptica cuspidata basi acuta. Pedunculus ovario brevior, flore inter minores. Calycis laciniae tubo triente breviores, appendicula brevi.

Arbor 8–10-metralis, coma globosa aut dilatata. Folia juniora nervis subtus puberula, aetate provectiore glabra punctulato-pellucida 8–13 cm. longa 4.5–6 cm. lata, nervis lateralibus utrinsecus 8–9, petiolis 1.5–2.5 cm. longis, stipulis aristuliformibus aegre 1 mm. longis glabris. Pedunculus 4–7 mm. longus. Calycis tubus 4–6 cm. longus, laciniae 3–4 cm. longae, appendicula 3–4 mm. longa. Petala 3 cm. longa. Filamenta 17–19 mm. longa, antheris 20–23 mm. longis. Ovarium 9–12 mm. longum, stigmate supra petala paulo exserto. Capsula 3–4.5 cm. longa, valvis dorso planis, seminibus oblongis 11 mm. longis 3 mm. latis obtusis, testa 4 mm. longa, ala basi involuta incrassata latere altero producta.

Costa Rica, Prov. San José: Río Torres, San Francisco de Guadalupe, alt. 1170 m., Jun. 1893, *Ad. Tonduz*, n. 8005 (Typus); Apr. 1894, *John Donnell Smith*, n. 4801 ex Pl. Guat. etc. quas ed. Donn. Sm.; Oct. 1898, *Ad. Tonduz*, n. 7445 ex Pl. Guat. etc. quas ed. Donn. Sm.: Río Tilirí, Alajuelita, alt. 1000 m., Aug. 1894, *Ad. Tonduz*, n. 8915: Río Virilla, San Juan, alt. 1000 m., Aug. 1896, *Ad. Tonduz*, n. 7285 ex Pl. Guat. etc. quas ed. Donn. Sm.: San José, Nov. 1898, *H. Pittier* (numero deficiente).

Hauyae ad dignoscendas facilius species liceat omnium hucusque cognitarum conspectum proponere.

Sect. I. SESSILIFLORAE Donn. Sm. et Rose.—Flos arcte sessilis.
A. Calycis laciniae inappendiculatae. *H. elegans* Moç. et Sessé
B. Calycis laciniae appendiculatae.
1. Appendiculae 3–4 mm. longae.
a. Capsularum valvae dorso carinatae. *H. cornuta* Hemsl.
b. Capsularum valvae dorso planae.
H. microcerata Donn. Sm. et Rose
2. Appendiculae 10–15 mm. longae.
a. Calycis laciniae tubo fere aequilongae.
H. Rodriguezii Donn. Sm.
b. Calycis laciniae tubo multo breviores.
† Capsula 3.5 cm. longa.
H. quercetorum Donn. Sm. et Rose
†† Capsula 7–8 cm. longa.
* Folia ex orbiculari-cordato ovalia.
H. ruacophila Donn. Sm. et Rose
** Folia ex oblongo-ovato oblongo-obovata.
H. lemnophila Donn. Sm. et Rose

Sect. II. PEDUNCULATAE Donn. Sm. et Rose.—Flos distincte pedunculatus.
A. Pedunculus ovario multo longior. *H. Heydeana* Donn. Sm.
B. Pedunculus ovario brevior vel ei subaequilongus.
1. Calycis laciniae inappendiculatae. *H. Bárcenae* Hemsl.
2. Calycis laciniae appendiculatae. *H. lucida* Donn. Sm. et Rose

Sicydium (§ EUSICYDIUM Cogn.) **Tuerckheimii** Donn. Sm.—Folia maxima oblongo-ovata sensim acuminata supra scabridiuscula subtus pubescentia. Flores masculi in paniculam amplissimam diffuse ramosissimam foliis reductis bracteatam digesti glabri minimi. Laciniae calycinae cum corollinis bis longioribus lanceolato-ovatae. Filamenta antheris aequilonga.

Suffruticosum, caulibus cirrhis paniculis sulcatis et petiolis glandulari-pubescentibus fuscis. Folia coriacea integra pedato-7-nervia transversim venosa 12–16.5 cm. longa 7.5–10.5 cm. lata, sinu basilari subrectangulari 1.5–2.5 cm. lato 1–1.5 cm. profundo, petiolis 2–3 cm. longis. Cirrhi 8–14 cm. longi apice bifidi. Paniculae, saltem eae florum masculorum, 3–4 dm. longae, ramis divaricatis bractea foliacea 1–3 cm. longa sustentis, inferioribus 1–1.5 dm. longis, bracteolis lanceolatis petiolatis 10–14 mm. longis, vel linearibus 2–5 mm. longis, pedicellis plerumque confertis capillaribus 1–2.5 mm. longis supra medium articulatis, floribus 3 mm.-diametralibus. Calycis tubus incrassatus patelliformis in sicco nigricans. Corollae laciniae 1 mm. longae reticulatae in

sicco flavicantes. Stamina 0.5 mm. longa. Flores feminini fructusque deficiunt.

In fruticetis, Cubilquitz, Depart. Alta Verapaz, Guatemala, alt. 350 m., Jul. 1907, *H. von Tuerckheim* (n. II. 1914).

Geophila pleuropoda Donn. Sm.—Tota pilosa. Folia petiolis bis longiora orbiculari-cordata obtusissima. Pedunculi pseudo-axillares folia aequantes vel bis fere superantes, floribus in capitulo subsessilibus quam bracteae involucrantes foliaceae longioribus. Calycis tubus segmentis triente brevior. Corolla calyce altero ţanto vel ultra longior. Antherae brevissimae.

Caules petioli pedunculi bracteae flores pilis patentibus bulbosis articulatis purpurellis conspersi. Folia membranacea pellucida utrinque praesertim supra bulboso-strigillosa subtus purpurascentia 2–3.5 cm. longa atque lata, nervis lateralibus utrinque 5–6, petiolis 1–1.5 cm. longis, stipulis caducis. Pedunculi primum terminales deinde caule producto axillares singuli 3.5–5 cm. longi, capitulo hemisphaerico absque corolla 6–7 mm. alto 5–8-floro, bracteis 2 oblongo-ovatis vel oblongo-lanceolatis in petiolum decurrentibus 6–7 mm. longis cito caducis, pedicellis vix 1 mm. longis, floribus 4–5-meris bracteola lineari 3 mm. longa sustensis. Calycis tubus 2 mm. longus discum vix superans, segmenta lanceolato-oblonga 3 mm. longa erecto-patentia, alterna saepe minora. Corolla 10–12 mm. longa triente lobata, tubo toto infundibuliformi intus glabro, lobis ovato-oblongis obtusis erecto-patentibus. Filamenta 2 mm. longa, antheris oblongo-ellipticis 1 mm. longis semiexsertis. Stylus filiformis, ramis 2 mm. longis inclusis totis papillosis. Drupa ignota.

Secus semitam inter Secanquím et Sepacuite, Depart. Alta Verapaz, Guatemala, alt. 1220 m., Febr. 1905, *George P. Goll* (numero deficiente).—Typus in herbario Musei Nationalis sub numero proprio 860647 servatur.

Tabernaemontana (§ EUTABERNAEMONTANA K. Schum.) **Deamii** Donn. Sm.—Folia elliptico- vel obovato-lanceolata apice contracto-acuminata deorsum attenuata. Thyrsi laterales folia subaequantes. Calyx inter minimos fere partitus. Corollae tubus cylindraceus gracilis rectus calyce sexies longior lobos proprios subaequans. Antherae sessiles totae fere exsertae. Discus nullus. Stylus elongatus. Folliculi obovoidei cuspidato-acuminati basi acuti.

Frutex 3-metralis omnino glaber. Folia pergamentacea nitida 9–12 cm. longa 2.5–4 cm. lata apice ipso obtusiuscula in eodem jugo saepius inaequimagna, nervis lateralibus utrinque 16–19 sub margine arcuatis et venis erga lucem inspectis pellucidis, petiolis 7–12 mm. longis. Thyrsi 10–12.5 cm. longi, cymulis dichotomis, pedicellis 10–13 mm. longis basi bracteatis. Calyx 2.5 mm. longus, segmentis paene sejunctis obtuse ovatis basi 4–5-glandulosis.

Corollae in sicco albae tubus 15–16 mm. longus 2 mm.-diametralis faucibus pubescens ore tuberculis 10 munitus, lobi dolabriformes apice rotundati. Antherae coeruleae 3 mm. longae ultra medium bifidae. Stylus 10–12 mm. longus, stigmate 5-apiculato inferne membrana dilatato. Folliculi cuspidę 1 cm. longa addita 6.5 cm. longi cartilaginei nitidi pallescentes 4-costati, seminibus ellipsoideis 5–7 mm. longis striatis ad hilum sulcatis, funiculis pulposis.—Secundum methodum Schumannianam gregi AaaII$_3$** adscribenda.

Secus fluvium *Montagua* prope Gualán, Depart. Zacapa, Guatemala, alt. 190 m., Jun. 1909, *Charles C. Deam*, n. 6282.

Lisianthus quichensis Donn. Sm.—Folia lanceolato-oblonga utrinque subsensim acuteque angustata sessilia amplexicaulia. Cymae longe pedunculatae laxe longeque ramosae. Calycis elongati segmenta ecarinata. Corolla calyce 4-plo fere longior, tubo a basi circiter ad trientem altitudinis sensim angustato et ibidem staminifero subinde infundibuliformi, lobis brevibus erectis. Genitalia exserta.

Suffrutex bimetralis glaber, ramis ramulis inflorescentiae axibus teretibus pallido-stramineis, internodiis folia paulo excedentibus, nodis membrana lineari interpetiolari marginatis. Folia pergamentacea 10–13.5 cm. longa 2.5–3 cm. lata, nervis lateralibus utrinque binis parum manifestis. Cymae pedunculis 5–8 cm. longis computatis 9–17 cm. longae ter quaterve trichotomae, pedicellis 4–7 mm. longis. Calyx 10 mm. longus usque ad $\frac{4}{5}$ partitus, segmentis lineari-lanceolatis filiforme attenuatis hyalino-marginatis. Corolla in sicco flavicans 36–38 mm. longa, tubo tertia parte inferiore crebre nervato, lobis cuspidato-ovatis 5 mm. longis. Stamina ad 11–12 mm. supra basin corollae inserta, filamentis inaequilongis 22–26 mm. longis, antheris exsertis oblongis erectis muticis. Discus nullus. Ovarium oblongo-ovoideum 6 mm. longum, stylo stamina 4 breviora aequante, stigmate capitato obscure bilobo. Capsula ignota.—A. *L. acuminato* Perk. proximo differt praesertim foliis angustioribus, calyce elongato, genitalibus exsertis.

Río Negro, Depart. Quiché, Guatemala, alt. 1100 m., Apr. 1892, *Heyde et Lux*, n. 2921 ex Pl. Guat. etc. quas ed. Donn. Sm. (Sub *Leiantho brevidentato* Hemsl. olim distributus.)

Lisianthus meianthus Donn. Sm.—Folia oblongo-ovata superne tenuiter deorsum contractius acuminata sessilia amplexicaulia 5-plinervia. Cymae corymbiformes laxiflorae, floribus minimis. Calycis segmenta leviter carinata. Corollae hypocraterimorphae tubus ultra ovarium tenuis faucibus staminiferis vix dilatatus calyce atque lobis propriis bis circiter longior. Genitalia exserta.

Suffruticosus dense ramosus. Rami teretes cum ramulis et inflorescentiae axibus subquadrangularibus pubverulentes et fusci, internodiis elongatis, nodis linea elevata interpetiolari marginatis. Folia pergamentacea 6–10 cm. longa

2.5–3.5 cm. lata, nervis subtus conspicuis longe ascendentibus. Cymae obdeltoideae 7–11 cm. longae repetitus trichotomae, pedicellis vix 1 mm. longis. Calyx 4–5 mm. longus paulo ultra medium fissus, segmentis lanceolatis hyalino-marginatis. Corollae in sicco luteae tubus 10 mm. longus dimidio superiore tenuiter cylindraceus fibroso-nervatus, lobi oblongo-elliptici 4–5 mm. longi sub anthesi expansi. Stamina ad 2 mm. infra os corollae inserta, filamentis aequalibus 3.5 mm. longis, antheris nec recurvis nec apiculatis. Discus nullus. Ovarium calycem subaequans, stylo staminibus aequilongo, stigmate peltato. Capsula oblonga 7 mm. longa reliquiis fibrosis tubi corollae marcidae vestita.

Sacolal, Depart. Alta Verapaz, Guatemala, alt. 915 m., Jan. 1889, *H. von Tuerckheim*, n. 1436 ex Pl. Guat. etc. quas ed. Donn. Sm. (Sub *Leiantho saponarioide* Griseb. olim distributus.)

Solanum (§ MICRACANTHA Dun.) **purulense** Donn. Sm.—Folia bina ternaque integra nitida pilis sparsis stellatis scabriuscula, altero uti alterum paulo minus lanceolato utrinque praesertim superne acute attenuato, tertio 2–4-plo minore elliptico utrinque acuminato. Racemi laterales stellato-tomentosi, rhachi parce aculeata, pedicellis flore dimidio brevioribus. Calyx inermis.

Rami sarmentosi super frutices reclinati lignosi teretes 5 mm.-crassi aculeati glabri purpurascentes apice cum foliis nascentibus stellato-fulvoque-tomentosi, aculeis stramineis e basi compressa 2.5 mm. longa uncinatis 2 mm. longis. Folia dua majora 11–18 cm. longa medio 3.5–6 cm. lata, pilis utrinsecus valde dissitis, costa subtus arcte aculeata, nervis lateralibus utrinque 6–8 subtus parce aculeatis, petiolis 1–2 cm. longis dense aculeatis, folio tertio 3–6 cm. longo 1.5–3 cm. lato breviter petiolato. Racemi 5–6 cm. longi secundiflori, pedicellis 8–10 mm. longis cernuis. Calyx stellato-tomentosus hemisphaericus 4 mm. altus triangulari-dentatus. Corollae rotatae segmenta linearia 18–19 mm. longa 2 mm. lata extus stellato-tomentosa. Filamenta 1 mm. longa, antheris linearibus 12–13 mm. longis apice biporosis. Bacca ignota.—Ad *S. lanceaefolium* Jacq. accedens.

In fruticetis ad Purulá, Depart. Baja Verapaz, Guatemala, alt. 1600 m., Apr. 1907, *H. von Tuerckheim*, n. II. 1751.

Alloplectus metamorphophyllus Donn. Sm.—Folia quam maxime disparia, altero magno elliptico utrinque acuminato perlonge petiolato, altero nano stipulaeformi lanceolato-lineari coccineo prophylla dua aflora sibi ipso omnino similia fulciente. Corymbus in axilla folii majoris subsessilis umbelliformis dense congestiflorus, bracteis bracteolis calycis segmentis supra medium subulato-laciniatis coccineis praeter lineam dorsalem glabris.

Suffrutex in truncis putridis epiphytalis nodis radicantibus longe repens, caule striato glabrescente erubrescente. Folium in pare majus nascens

utrinque densissime stramineo-holosericeum, adultum praesertim subtus glabrescens membranaceum mucro-denticulatum 17 22 cm. longum 8–10 cm. latum, petiolo gracili 7–10 cm. longo glabrescente. Folium nanum cum prophyllis paulo altius sitis lateralibus sessile erectum filiforme productum 3–4 cm. longum 6–8 mm. latum membranaceum praeter lineam dorsalem glabrum. Corymbus subglobosus 2.5–4 cm.-diametralis, pedunculo 6–8 mm. longo et axibus pubescentibus, pedicellis 3–10 mm. longis, bracteis ovalibus vel oblongo-ellipticis 14–16 mm. longis, bracteolis lineari-lanceolatis 15–18 mm. longis subulato-productis. Calycis segmenta fere sejuncta aequalia lanceolato-linearia longe subulato-producta 12–16 mm. longa, laciniis 3–5 mm. longis. Corolla nondum satis evoluta pilosa calyce brevior leviter ventricosa basi vix gibbosa ore obliqua, lobis rotundis brevibus. Antherae liberae breves, loculis parallelis distinctis. Disci glandula solitaria obtuse ovata 2 mm. longa. Ovarium pilosum acuminato-ovoideum 3 mm. longum, stylo 5 mm. longo, stigmate bilobo. Fructus coriaceus glaber ovato-globosus 6 mm. longus indehiscens, seminibus funiculo capillari affixis. Flores evoluti ignoti.—Species anormalis.

La Palma, Prov. San José, Costa Rica, alt. 1500–1600 m.: *Adolfo Tonduz*, Sept. 1896, n. 10884; Aug. 1898, n. 12469: *William R. Maxon*, Maj. 1906, n. 364.

Besleria (§ PARABESLERIA Hanst.) **pycnosuzygia** Donn. Sm.—Internodia brevissima. Folium alterum altero subduplo majus coriaceum discolor integrum supra glabrum subtus puberulum oblique lanceolatum utrinque acutum, nervis lateralibus validis utrinsecus 5–6 sub angulo angusto longe ascendentibus. Pedicelli aggregati internodio petiolo flore paulo breviores. Corolla calyce subtriplo longior. Ovarium pilosum.

Suffrutex, caule simplice tetragono nodis incrassato, internodiis 1.5–2.5 cm. longis, partibus novellis canescentibus. Folium in pare majus 10–14 cm. longum 3.5–4.5 cm. latum inaequilaterale, nervis lateralibus subtus prominentibus supra impressis, petiolis 1–2 cm. longis. Pendunculus nullus, pedicellis circiter 6–8-nis 8–18 mm. longis puberulis. Calycis partiti extus puberuli intus pilosi segmenta oblongo-ovata obtusa 7 mm. longa integra margine scariosa, postico minore declinato. Corolla coccinea sericea 21–24 mm. longa, tubo recto superne leviter ampliato vix ventricosa basi defracto postice gibbo, lobis rotundatis subaequalibus. Stamina ad 4 mm. supra corollae basin inserta, antheris cohaerentibus transversim ellipticis, loculis orbicularibus. Discus subaequalis 2 mm. altus antice interruptus. Ovarium ovoideum 3 mm. longum, stylo 1.5 cm. longo. Fructus ignotus.

In silvis ad La Palma, Prov. San José, Costa Rica, alt. 1459 m., Sept. 1898, *Adolfo Tonduz*, n. 12545.

BALTIMORE, MARYLAND

APPARATUS FOR THE STUDY OF COMPARATIVE TRANSPIRATION

EDGAR N. TRANSEAU

(WITH FIVE FIGURES)

The quantitative study of the ecological factors of the habitat naturally leads to a similar investigation of the responses of the "growth-forms" to these elements of the habitat. Thus the investigation of the comparative evaporation of various local habitats has led to a complementary study of the comparative rates of transpiration of the plants occurring in them. In this latter work an effort has been made to obtain graphs of the hourly transpiration rates under a great variety of conditions of temperature, light, and humidity. For comparative purposes these data are being collected (1) by the synchronous exposure of several plants, and (2) by determining the ratios between the transpiration rate and the rate of evaporation from a standard vaporimeter.

It is evident that for conducting a study of this kind, in which data regarding the effects of stimuli and latent periods are essential, the determination of the water losses by the method of weighing at intervals of several hours is, to say the least, unsatisfactory. A very perfect apparatus for the automatic weighing and recording of evaporation rates has been described by GANONG in this journal.[1] For comparative purposes, however, several of these instruments are required, making the cost beyond the means of at least some laboratories. The following apparatus is essentially a modification of the Ganong transpirograph, developed for the special purpose of comparative work. Its efficiency, combined with its comparatively small cost, has made it seem worth describing in advance of the discussion of the data which are being obtained by its use.

The complete outfit, as shown in fig. 1, consists of a hygrothermograph, a chronograph, chemical balances, weight droppers,

[1] New precision appliances for use in plant physiology. BOT. GAZETTE **39**:145. 1905.

and irrigators. Of these the chronograph, the weight droppers, and the irrigators are new forms of well-known devices.

THE CHRONOGRAPH.—Where synchronous records are desired, it seemed that a chronograph having several pens to mark on the same sheet of paper would be more desirable than several separate instruments, not only on account of the decreased cost, but also

FIG. 1.—Complete apparatus for recording comparative transpiration data: *1*, combined hygrograph and thermograph; *2*, weight dropper; *6*, irrigator; *7*, chronograph.

because the errors of the clocks would be eliminated. The chronograph shown in fig. 1 has an eight-day movement attached to a horizontal cylinder 15 cm. long and 15 cm. in diameter. The record is made by pens which mark a continuous line except when drawn aside by an electro-magnet. At present the instrument bears four pens, but it is so constructed that four more may be added on the same side, thus increasing its capacity to eight synchronous records. By lengthening and shortening the hairspring the space traversed by the pen in one hour may be varied from 2 to 5 mm. In the

latter case the cylinder makes a complete revolution in about four days. A strip of ordinary millimeter cross-section paper is used for the record sheet. In class experimentation this recording clock has a variety of possible uses aside from this particular experiment.

FIG. 2.—Weight dropper and circuit-closing device

THE WEIGHT DROPPERS.—As in the Ganong transpirograph, the recording of the water losses depends upon an electrically actuated mechanism which drops a definite weight in the form of a one-fourth-inch ball upon the scale pan whenever the pan reaches a certain height. As shown in fig. 2, the circuit-closing device consists of two platinum points just beneath the delivery tube

which dip into a small cup of mercury on the scale pan whenever a balance is established. The one gram weights are too heavy to obtain satisfactory records from many of the extreme xerophytes. For these plants I am using hollow brass balls standardized to 0.4 gm. These are not as light as could be desired, but they are better than the gram weights. To be very satisfactory for comparative purposes, the interval between records should not exceed two hours. Where great differences exist between day and night rates, I have used the fractional weights at night and the gram weights during the day.

THE IRRIGATORS.—Two points which became evident in the early experiments are that the water content of the soil of the plants to be compared must be essentially the same, and that the water content must be essentially the same throughout the experiment. The ordinary method of watering at 24-hour intervals did not give satisfactory results in some instances. In one experiment the ratio between two plants on successive days was reversed on account of differences in soil water content. To avoid errors of this kind the principle of irrigating plants by porous cups suggested by LIVINGSTON[2] was brought into use, and the apparatus shown in fig. 3 was constructed. It consists of a slender porous cup similar to those used in my vaporimeters.[3] This is readily introduced into the soil of a 3-, 4-, or 5-inch pot by removing a core of soil with

FIG. 3.—Details of the irrigator, showing porous cup, water reservoir, and connections.

[2] A method of controlling plant moisture. Plant World 11:39. 1908.

[3] A simple vaporimeter. BOT. GAZETTE 49:459. 1910.

a cork borer slightly smaller than the porous cup. The cup is connected by glass and rubber tubing to a horizontal reservoir made of a flat-sided "specimen bottle." The reservoir is supported at the side of the scale pan by a light wire bracket, attached to a flat cork upon which the aluminum shell containing the plant rests. The second tube at the upper end of the porous cup affords an easy method of filling the cup. After the water has been drawn up, this tube is sealed with cement. The air needed to replace the water in the reservoir enters through the stopper by a capillary tube. By extending this capillary tube beneath the water level, the rate at which the water is removed may be approximated by the rate at which air bubbles enter. This may yield interesting results concerning the relative time of the absorption and transpiration maxima. It is of course open to the same objections as the Reinke method of determining the relative rate of photosynthesis in submerged plants.

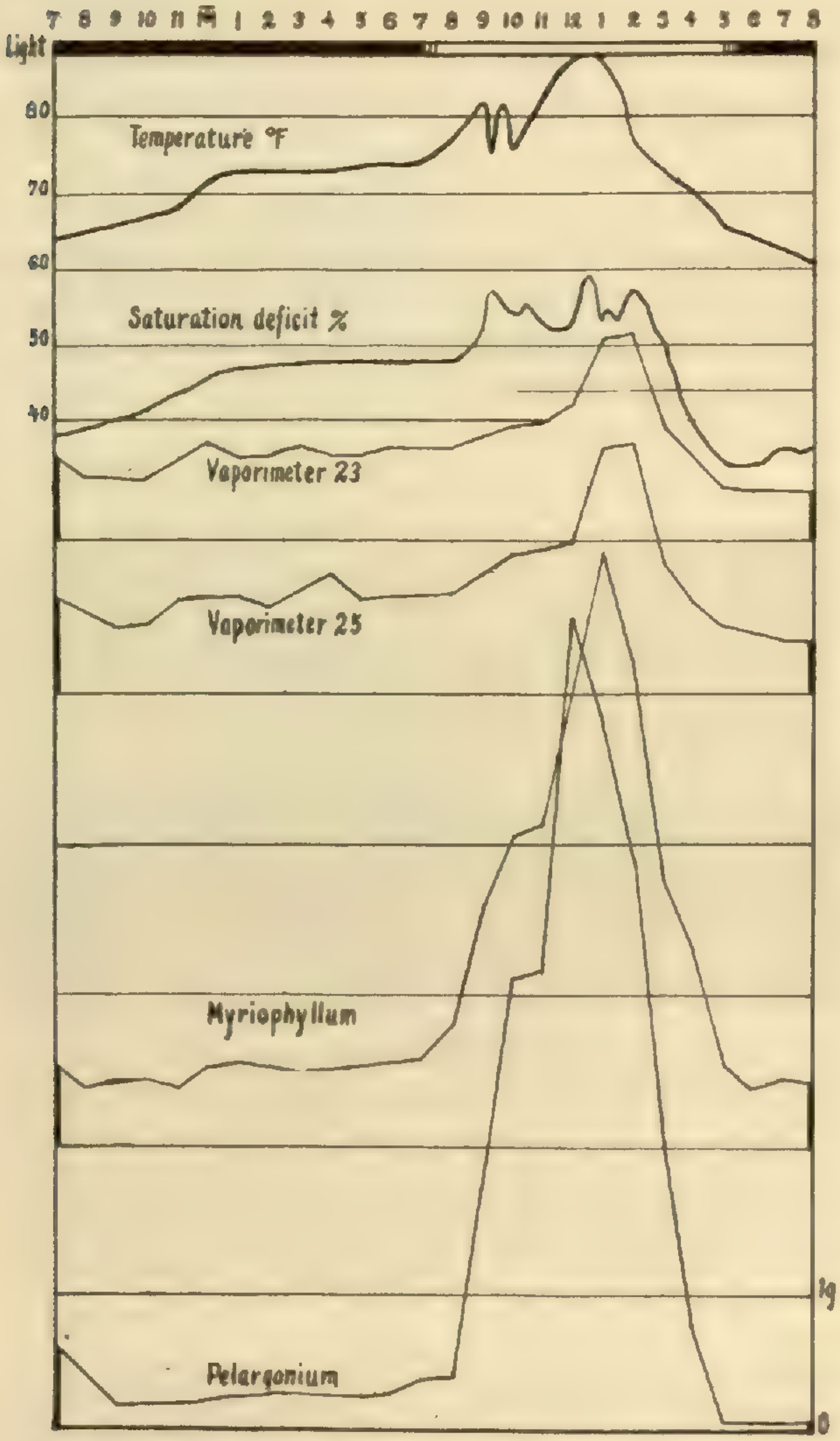


FIG. 4.—Graphs for part of the record of experiment 8.

The aluminum shells devised by GANONG[4] are very satisfactory for inclosing the pots. The 15 cm. shell seems to be the most satisfactory to use, regardless of the size of the pot, because of the larger volume of air inclosed. I have no quantitative data to prove

[4] BOT. GAZETTE 41:212. 1906.

this, but the plants appear to withstand the experimental conditions perfectly in this largest shell and not so perfectly in the more closely fitting ones. When the irrigators are used, it is convenient to have a 1 cm. hole in the side of the shell closed by a cork through which the air may be changed at intervals by means of a small bellows. This avoids the necessity of removing the roof from the shell during

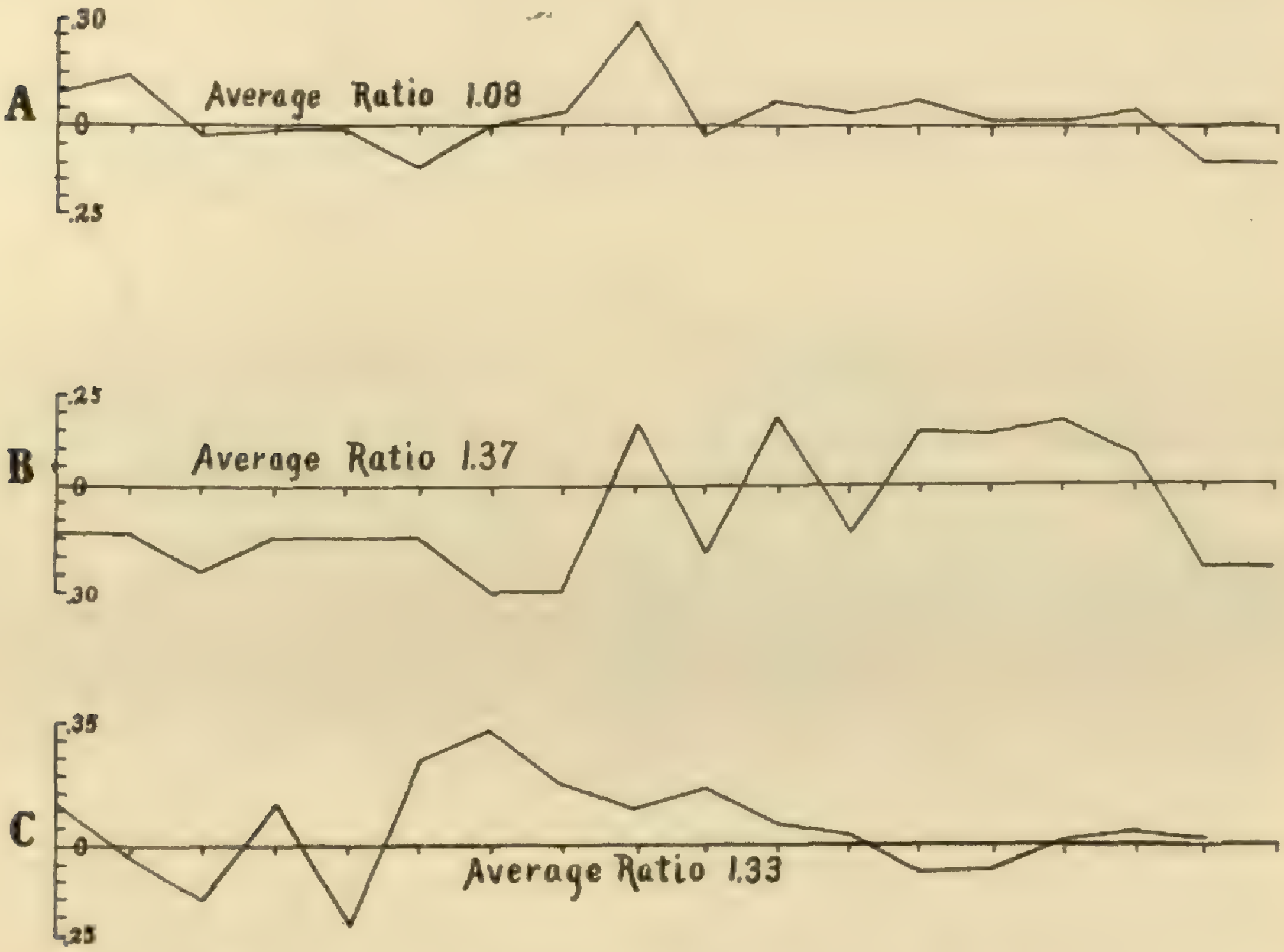


FIG. 5.—Departures from the average ratio between two synchronous records calculated to 2-hour periods: *A*, two vaporimeters; *B*, two irrigated pelargoniums; *C*, two pelargoniums watered at 24-hour intervals; average ratios calculated from the total water losses.

the experiment. The smaller pots are brought to the upper level of the shell by being placed on a strip of aluminum bent in the form of a W. This raising of the pot above the level of the water reservoir is necessary to prevent flooding of the soil.

In constructing the graphs from the actual records and in calculating the ratios, an engineer's slide rule has been found to be a great time saver. Fig. 4 shows the complete record for a portion of experiment 8.

To determine to what extent two records may be expected to

coincide by this method of recording, six experiments of two to five days' duration have been performed. The graphs shown in fig. 5 exhibit the actual ratios for 2-hour intervals in comparison with the average ratio for the entire experiment, for synchronous records of two vaporimeters (*A*), two irrigated pelargoniums (*B*), and two pelargoniums watered at 24-hour intervals (*C*). These partial records are sufficient to show that variations in the ratios between records must be greater than 0.3 in order to be significant. It will be readily seen that the variations in the actual records sufficient to produce this variation in the ratios are very small fractions of a gram in most instances. There are various explanations for these minor irregularities: the impossibility of estimating the hourly loss accurately when the gram-interval extends over several hours; shadows made by the framework of the greenhouse; differences in exposure to light; differences in irritability, etc. Whatever their causes, they must not be overlooked in comparing plants of different species and different habitats.

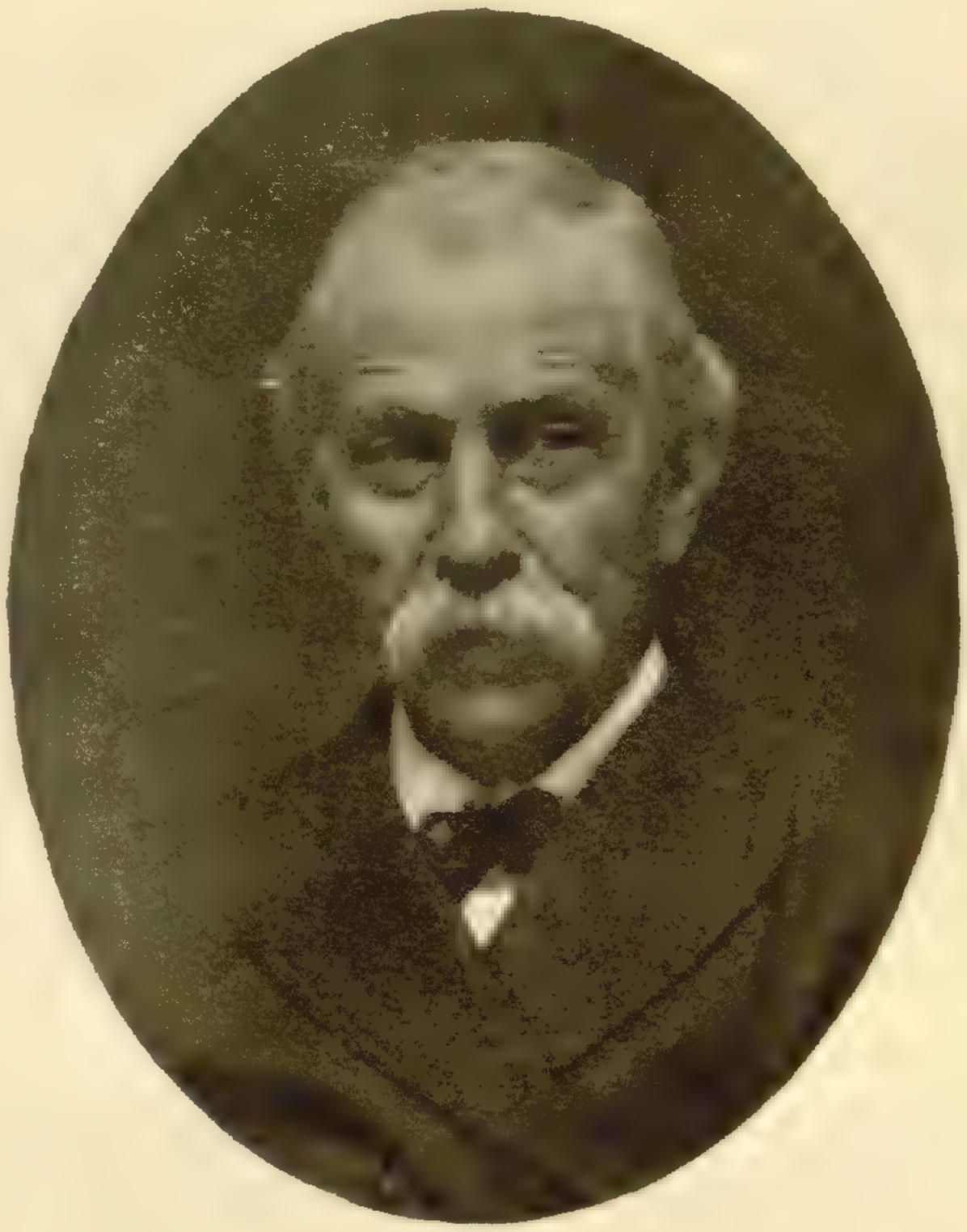
EASTERN ILLINOIS STATE NORMAL SCHOOL
CHARLESTON, ILL.

BRIEFER ARTICLES

EDWARD PALMER

(WITH PORTRAIT)

Dr. EDWARD PALMER died at his home in Washington, D.C., April 10, 1911, after an illness of a few days. He was an exceptional explorer and collector, who in the field of botany alone is distinguished as the discoverer of 1,162 new species of flowering plants, with many more of his last collecting still remaining to be described. At least 200 plants discovered by him bear his name, and will continue as witnesses to his wonderful activity.



He was the son of a professional florist and horticulturist, of Hockwold cum Wilton, in the county of Norfolk, England, where he was born January 12, 1831. Coming to this country at the age of 18 he settled at Cleveland, Ohio, where he formed the acquaintance of Dr. JARED KIRTLAND, one of the most eminent scientists of his day, and one of the earliest members of the American Academy of Science. From him he learned the art of collecting and preserving objects of natural history, thus laying the foundation of his future career, and through KIRTLAND'S influence he was in 1853 appointed naturalist of the "Water Witch," on her celebrated expedition to Paraguay, which led to our war with that country.

After his return to the United States, he was appointed collector in the Geological Survey of California, paying especial attention to the marine invertebrates of the California coast. In 1862, when President Lincoln called for extra troops, he offered his services to his country, and

after a time was appointed acting assistant surgeon at various posts in the West and Southwest, continuing to serve after the close of the war on frontier stations in the Indian country in Arizona and the Indian Territory. In connection with his work of attending the sick, he familiarized himself with the properties and uses of the medicinal herbs growing in the vicinity of his station, and he occupied his moments of leisure in making collections of animals and plants for the Smithsonian and other institutions.

In March 1869 he was sent by the Commissioner of Agriculture on a mission to New Mexico and Arizona, to report on the agricultural resources, commercial products, climate, and fertility of the soil, and the general habitable features of the Southwest. He afterward carried on archaeological investigations in southwestern Utah, and made extensive botanical and zoological investigations in that region, assisted in his work by a circular letter given him by BRIGHAM YOUNG. The Commissioner of Agriculture, HORACE CAPRON, in his report for 1870, called special attention to the value of his work, and he was congratulated upon his success by such eminent botanists as Professor ASA GRAY, Dr. TORREY, and Dr. ENGELMANN, all of whom considered themselves fortunate in having valuable material collected by him.

From a scientific point of view, the most important exploration made by him was that of Guadalupe Island, never before visited by a naturalist. The bearing upon evolution of the remarkable fauna and flora of this island in the Pacific Ocean, off the coast of Lower California, is almost as important as that of the animals and plants of the Galápagos Archipelago, as demonstrated by DARWIN. Every bird in his collection from Guadalupe, except a single sea bird, proved to be new to science; and among the plants collected at this time there were 21 new species, the greater part of which have never since been found elsewhere.

Other important collections were made by him in southern California and across the border in Lower California. Here, in a great canyon of the Cantillas Mountains, he discovered a plant which proved to be the type of a new genus, named in his honor *Palmerella* by Professor GRAY, who stated that he did so in acknowledgment of Dr. PALMER'S "indefatigable and fruitful explorations of the botany of the southwestern frontiers of the United States, from Arizona to the islands of Lower California, in which region he has accomplished more than all his predecessors."

The latter part of Dr. PALMER'S life has been devoted chiefly to exploration in Mexico, and the results have been published chiefly in

the Proceedings of the American Academy of Arts and Sciences, and in the publications of the United States National Museum. His collections, both botanical and ethnological, have been remarkable, not for the prettiness of the various objects, but for the completeness of the material and the care shown in his notes.

He continued his chosen work to the very end. His last exploration was in 1910, in the vicinity of Tampico, on the gulf coast of Mexico. After his return he occupied himself in assorting and distributing his material. On the occasion of the eightieth anniversary of his birth, the Botanical Society of Washington held a special meeting in his honor, at which a paper on his life and work by the author of the present sketch was read, together with letters written by various eminent men of science not residing in Washington. During the meeting of the society Dr. PALMER was seated in the place of honor, and at the close of the exercises he was presented with an appropriate birthday gift as a token of the appreciation of the members of the society of his important life-work. The venerable traveler received the congratulations of those present with tears streaming down his cheeks, doubtless realizing that this must be his valedictory.—W. E. SAFFORD, *Department of Agriculture, Washington, D.C.*

DEHYDRATING WITH ALCOHOL

(WITH FOUR FIGURES)

The difficulty which undergraduate students who take courses in histology find in giving regular attention to dehydration, led me to a search for an automatic method. Osmotic means were rejected because they are uncontrollable and give no indication of the stage of the process. Work on the principle of slowly adding alcohol of increasing strength to the tissue developed the simple apparatus shown in fig. 1. During the past two years this apparatus has been used for dehydrating all kinds of plant tissue for histology and embryology. It has also been used instead of glycerin in preparing algae to be mounted in Venetian turpentine.

The alcohol from the supply bottle drops from the lower end of the "capillary" *v* into the thistle tube, which conveys it to the bottom of the mixing tube *B*. The alcohol diffuses with the water in *B*, and the increase in volume is carried to the dehydrating tube *C* through the connecting tube *x*. Naturally, as more alcohol is added to *B*, the strength of the liquid passing into *C* increases, but as that in *B* is always

only slightly stronger than that in *C*, the tissues which are placed in *C* are not injured. In cases where extraordinary care is needed, it may be desirable to keep the tissues some distance from the opening through which the alcohol enters *C*. The siphon *y* removes the excess of

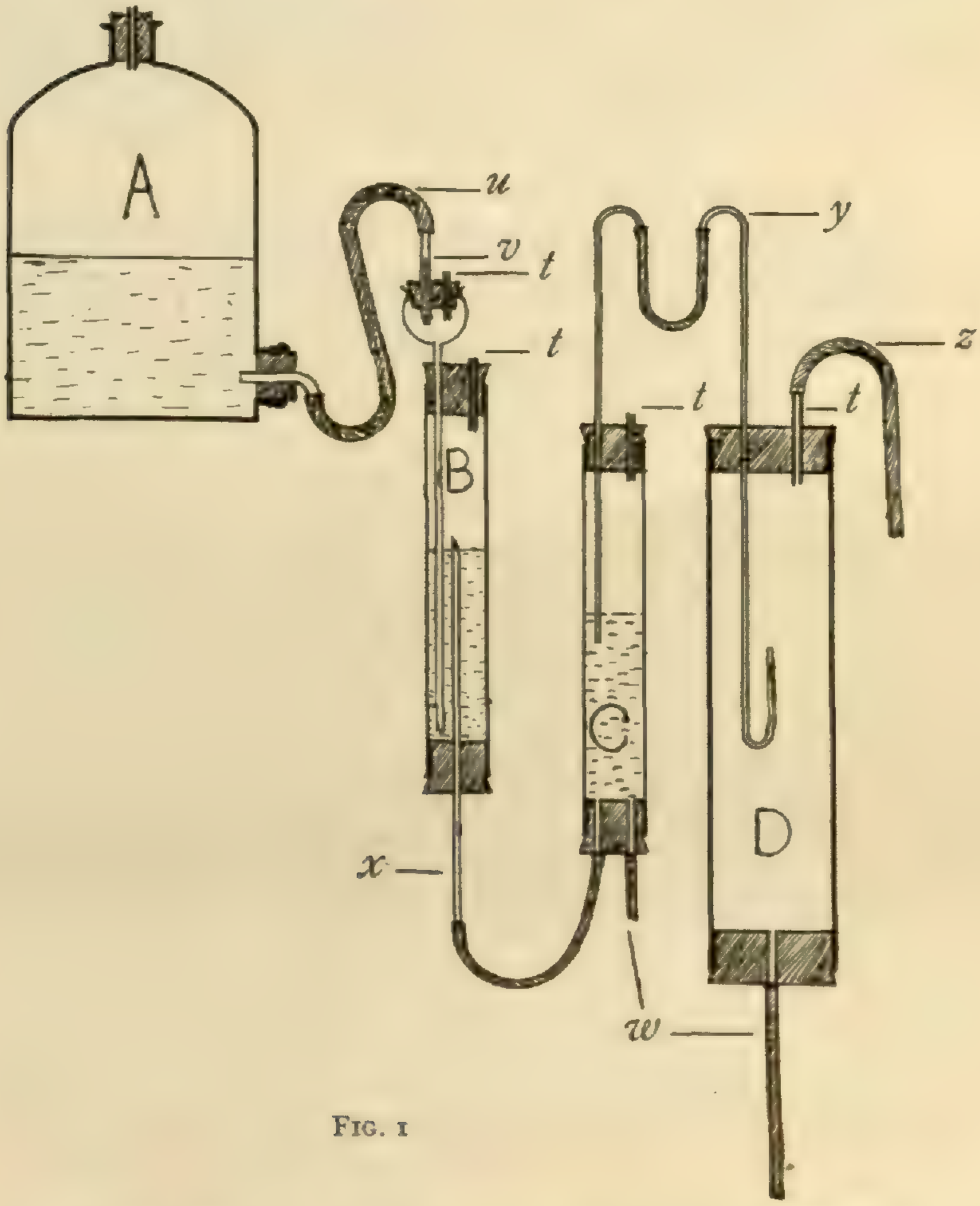


FIG. 1

FIG. 2

FIG. 3

FIGS. 1–3.—Fig. 1, *A*, supply bottle; *B*, mixing tube; *C*, dehydrating tube; *D*, waste tube; *t*, *t*, capillary tubes (air vents); *u*, supply tube; *v*, "capillary"; *x*, overflow; *y*, siphon; *z*, tube for starting siphon; fig. 2, "Capillary" on a larger scale: *n*, large tube; *m*, smaller tube, drawn to capillary (*p*) and sealed into lower end of *n*; fig. 3, washing jar with gauze neck.

dilute alcohol from *C*. The bent end of the siphon in the waste tube *D* prevents the automatic emptying of the siphon. When the apparatus is to be used, tissues and water are placed in *C*, and an equal volume of water is placed in *B*. The overflow *x* and the siphon *y*, which is filled by withdrawing the air from *D* through the tube *z*, are set to keep these volumes constant. The flow of alcohol is started by remov-

ing the "capillary" and supply tube from the thistle tube and letting them hang downward from the supply bottle for a minute to expel all the air from them.

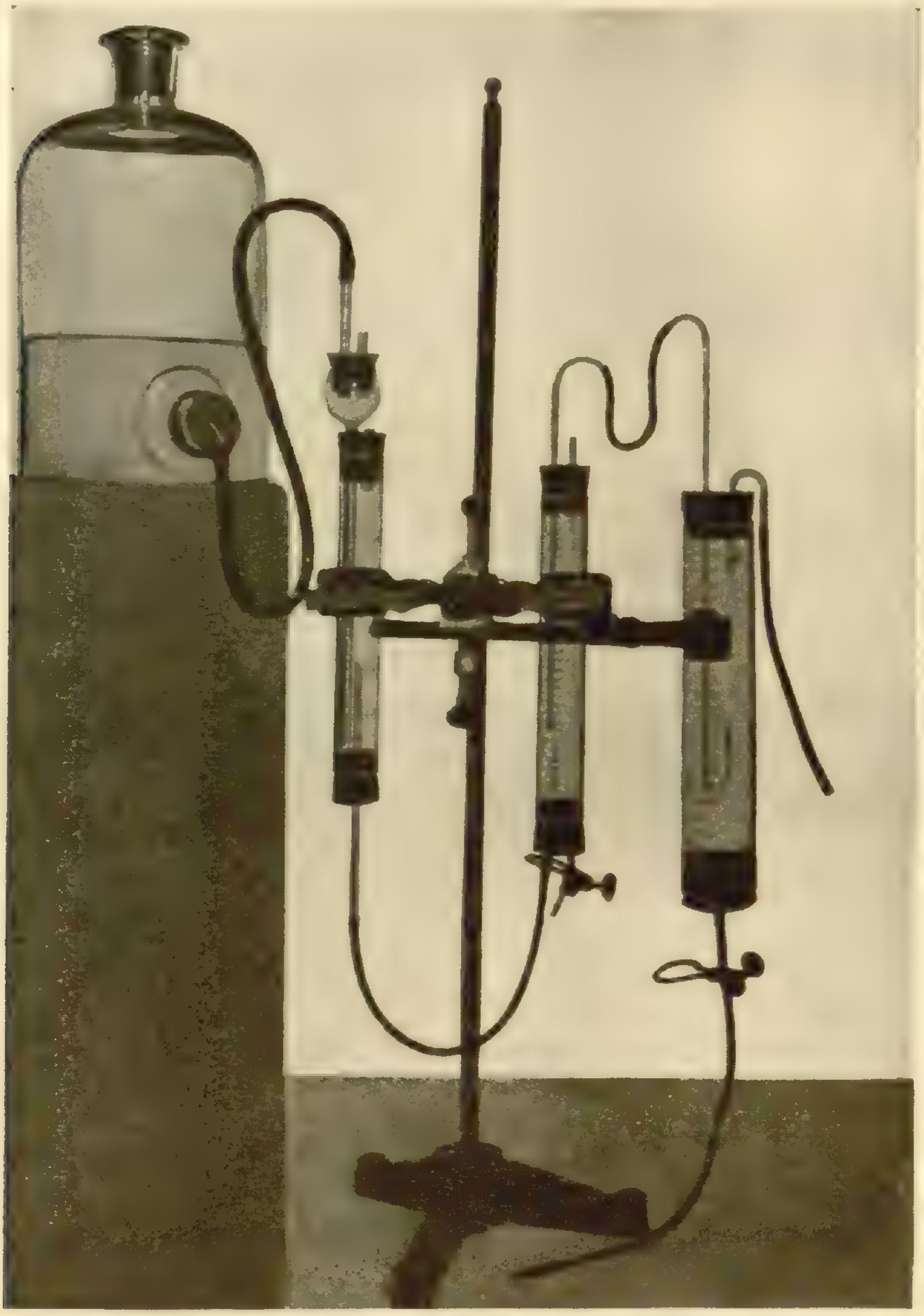


FIG. 4.—Photograph showing supports: to the stem of the double burette clamp, which holds the mixing and dehydrating tubes, is attached a single clamp which holds the waste tube.

Mathematical calculations, as well as numerous picnometer tests, show that the percentage of alcohol in *C* increases very steadily to about 75 per cent. Calling the contents of *C* one volume, the picnometer tests show that two volumes of 95 per cent alcohol will raise the strength of that in *C* to 70 per cent, three volumes to 85 per cent, and four to 92

per cent. However, most tissues may be taken from 85 per cent alcohol and covered with that remaining in *B*, and then transferred from that to either 95 per cent or absolute alcohol.

The flow of alcohol is insured against varying vapor pressures by the short capillary tubes in the stoppers which close the upper ends of the larger tubes, or if suitable capillary tubing cannot be obtained ordinary glass tubes nearly sealed at both ends will do quite as well. In either case the slightest amount of water in them renders them worthless. The "capillary" is shown at *v*, and enlarged in fig. 2. It is made by sealing within a larger glass tube a small one first drawn out to a very fine capillary. With a head of 40 or 50 cm. it should allow several drops of alcohol to flow per minute. If the flow is too slow, the small end of the fine capillary may be broken off with a pair of forceps. Otherwise the flow is regulated by raising either the supply bottle or the remainder of the apparatus, which is clamped on the ring stand. As a drop of alcohol from *v* per minute means 1 cc. per hour, and most material may be dehydrated in 40 hours or less, it is easy to adjust the flow, and the apparatus needs no further attention until its part of the process is complete. *B* and *C* may each conveniently be ordinary glass tubing 15 cm. long and 2.5 cm. in diameter. *D* is of similar material twice this diameter and 5 cm. longer. It is very convenient to have all three of these tubes graduated. The supply tube should be at least 6 mm. inside diameter, so that, when starting, the alcohol will readily replace the air in it; but, as the contents of the other connections are added to the waste alcohol and dehydration is delayed by the contents of *x*, these should not be over 1.5–2 mm. inside diameter. It seems that only the best antimony rubber tubing will withstand alcohol. Ordinary physicians' catheters, one large and two small, will furnish all of this tubing that is needed.

In practice it is convenient, after killing is complete, to tie the tissue with a label number in a square of fine silk gauze (chiffon). Knots are unnecessary; after the corners of the gauze are brought together a half dozen turns of very fine cotton thread will hold very well. A number of samples may then be washed very effectively under a small tap, in a jar the neck of which is provided with a cylinder of wire gauze as shown in fig. 3. After washing, the samples are transferred to the dehydrator and may afterward be kept in one or at least very few dishes until infiltrated with paraffin. The silk gauze also protects the samples from the air while they are being transferred to the imbedding dish, where it may be cut and the pieces of tissue and label properly arranged.—
W. A. WUILLSCHLEGER, *Nebraska Wesleyan University, Lincoln.*

CURRENT LITERATURE

MINOR NOTICES

Die Pflanzenstoffe.—WEHMER[1] has made readily available the known facts about the plant products (chemicals, drugs, enzymes, etc.) of the phanerogams. The plant families are arranged in the natural order, and under each the genera and species of which we have any chemical knowledge, along with the facts known and citations of literature establishing the facts. On the purely botanical side many facts of distribution are recorded. The work will prove of great value to plant chemists, pharmacists, and plant physiologists. A full index of the chemicals mentioned and a second one of the raw materials and plants greatly enhance the value of the book.—WILLIAM CROCKER.

Micrography of Javanese woods.—The third part of JANSSONIUS' micrography of the woods of Java has appeared,[2] and apparently completes this very laborious work, as it contains a general index to the two volumes. The plan of the work was described in the notice of the first part,[3] and a notice of the second part[4] indicated the further extension of the work. The present part, beginning in the midst of Meliaceae and closing with Moringeae, contains 100 species, the total for the two volumes being 329. Detailed descriptions of the vascular elements of so many species, including lists of reagents, sections, and material in each case, and also references to literature under each species, represent an amount and kind of work that few would care to undertake.—J. M. C.

Prodrome de la Flore Corse.[5]—Notwithstanding the long series of valuable contributions to systematic botany, both floristic and monographic, by which BRIQUET has enriched scientific literature, it is probable that he is chiefly

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[1] WEHMER, C., Die Pflanzenstoffe botanisch-systematisch bearbeitet chemische Bestandteile und Zusammensetzung der einzelnen Pflanzenarten Rohstoffe und Produkte Phanerogamen. 8vo. pp. xvi+937. Jena: Gustav Fischer. 1911. *M*35.

[2] JANSSONIUS, H. H., Mikrographie des Holzes der auf Java vorkommenden Baumarten; im Auftrage des Kolonial-Ministeriums unter Leitung von Dr. J. W. MOLL bearbeitet im Anschluss an "Additamenta ad cognitionem florae arboreae javanicae auctoribus S. H. KOORDERS et TH. VALLETON." Dritte Lieferung. 8vo. Vol. II, pp. 161–540. *figs. 49*. Leiden: E. J. Brill. 1911. *M*6.

[3] BOT. GAZETTE **43**:345. 1907.

[4] *Ibid.* **47**:416. 1909.

[5] BRIQUET, JOHN, Prodrome de la Flore Corse, comprenant les résultats botaniques de six voyages exécutés en Corse sous les auspices de M. EMILE BURNAT. Vol. I. Geneva: Georg & Co. 1910.

known, in America at least, by the devoted attention he has given to the cause of a better international agreement on the controversial subject of nomenclature. As reporter-general of two international congresses, he has won universal admiration for clarity and fairness, and has gained the warmest gratitude of his colleagues for the exceptional efficiency and energy, which, with great self-sacrifice, he brought to bear upon an exceedingly intricate, time-consuming, and unremunerative task.

It has been generally known that BRIQUET for the last ten years or more has been engaged, notwithstanding the serious interruptions to which we have alluded, in an intensive study of the Corsican flora. In order to gain ample collections and a first-hand familiarity with the floristic conditions, no less than six expeditions to Corsica were made by him and his associates. Not only were the more accessible parts of the island repeatedly visited, but the wilder portions of the interior, including primitive woodlands, still infested by brigands, were traversed and examined.

The publication now at hand is the first volume of what has been modestly styled a *Prodrome*. It is an imperial octavo of something over 650 pages, and contains, besides prefatory matter and bibliography, a critical catalogue of the vascular plants of Corsica from the Hymenophyllaceae to the Lauraceae, including 722 species and many varieties. Under each, the citation of literature, synonymy, and exsiccatae is exhaustive. Habital notes and comments on distinctive characters, distribution, environment, etc., abound, and at points keys are introduced to elucidate distinctions between plants of the Corsican flora and their nearest relatives found elsewhere.

Without the slightest depreciation of its other and more scientific merits, it may be safely said that no small part of the interest attaching to BRIQUET'S work will be found in the fact it exemplifies, probably in a higher degree than any other flora published to date, the conscientious application of the international rules of nomenclature by one specially trained in all their shades of meaning and intricate details.—B. L. ROBINSON.

NOTES FOR STUDENTS

Genetic studies in Oenothera.—The important deductions made by DEVRIES, from the results of a twenty-years' study of *Oenothera Lamarckiana* and its derivatives, have created an unusual interest in this species and its relatives. Numerous investigations have been made by many students, without any apparent exhaustion of the wealth of interesting phenomena presented. The oenotheras seem destined to yield results of great value for a long time to come, for the interest in the group grows greater rather than less with further study. The validity of some of DEVRIES'S conclusions rests upon the correctness of the assumption that *O. Lamarckiana* is a native species. Many diligent searches have been made in the effort to discover it in a natural habitat in America, but so far without success.

DAVIS[6] believes that *O. Lamarckiana* does not occur as a native species, but that it is a hybrid, probably between forms of *O. grandiflora* and *O. biennis*, and that it originated in European gardens, or that it may have occurred as a wild hybrid. To test this hypothesis he is making numerous crosses between different forms of these two species, and selecting those types among the hybrid progenies which most closely resemble *O. Lamarckiana*. He reports that all of the hybrid forms thus far produced by him differ from *O. Lamarckiana* in several important points, but that the resemblances of some of them to that species are such that the taxonomist would at least place these hybrids next to *O. Lamarckiana*. DAVIS is not convinced, by the evidence at hand, that the plants figured in certain old plates or described in various horticultural magazines of a century or more ago are to be safely referred to *O. Lamarckiana*, as they have been by several writers. The effort to synthesize *O. Lamarckiana* is being continued by the use of other biotypes of the two chosen species, and it is expected that some of these will offer a still closer approach to the desired result. Reports on these further studies will be awaited with the greatest interest, and especially regarding the capacity of any of the new forms to yield a series of true-breeding segregates, such as the forms derived from *O. Lamarckiana* which are now generally recognized as mutants.

All students of genetics who have handled the oenotheras in hybridization experiments appreciate the fact that they are quite anomalous in their hereditary behavior, and that they do not clearly follow the simple procedure usually observed in the hybrids of other plants and of animals. Under the circumstances, no far-reaching generalizations should be drawn from studies in the oenotheras except on the basis of extensive cultures and the most careful analysis of results. GATES[7] has made some features of *O. rubrinervis* and of a derivative from it, which he calls *O. rubricalyx*, the basis of generalizations regarding the nature of unit-characters, which appear to the reviewer not to observe this desired caution. *O. rubricalyx* differs from *O. rubrinervis* not only in amount of anthocyan in leaves and buds, but also to some extent in its distribution, the latter form having a red hypanthium, red midribs of the sepals, and red on the ventral surface of rosette-leaves and especially of their petioles, in which positions *O. rubrinervis* has a green or yellowish color. Nine cultures from self-fertilized *O. rubricalyx* gave in each case not only *O. rubricalyx*, but also *O. rubrinervis* offspring, though the ratios were not satisfactorily determined. The conclusion is reached that therefore *O. rubricalyx* is incapable of breeding true. The number of families is too small, however, to warrant this conclusion, for Mendelian expectation would allow six of the nine

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[6] DAVIS, B. M., Genetic studies on *Oenothera*. II. Some hybrids of *Oenothera biennis* and *O. grandiflora* that resemble *O. Lamarckiana*. Amer. Nat. **45**:193–233. *figs. 18.* 1911.

[7] GATES, R. R., Studies on the variability and heritability of pigmentation in *Oenothera*. Zeit. f. Ind. Abstam. Vererb. **4**:337–372. *pl. 1. figs. 5.* 1911.

parents to be heterozygous, and it puts no strain on the "errors of random sampling" to account for the remaining three as a purely chance result. Reciprocal crosses between *O. rubricalyx* and *O. Lamarckiana* seem to have resulted in each case in a progeny of *rubricalyx* and *Lamarckiana*, though the determinations were defective. The appearance of these two types in the first generation seems at first glance to be distinctly unlike Mendelian behavior, but if the *rubricalyx* plants used for the crosses were heterozygous, two types should have been expected in the progeny. The author uses the expression "alternative inheritance" for cases in which the two parental types appear in the F_1 and breed true in later generations. This new use of the expression "alternative inheritance" will result in confusion if it is adopted by others, since all Mendelian inheritance is "alternative," as the expression is now generally used among geneticists.

GATES is of the opinion that *O. rubricalyx* represents a progressive mutation from *O. rubrinervis*, and that it is not to be explained on the basis of the presence and absence hypothesis. For the simple and direct, though somewhat formal and figurative, terminology generally used in describing Mendelian behavior, GATES would substitute " a quantitative readjustment of the relation between the substances which by their chemical interactions produce anthocyan, and those which decompose it as soon as formed, or which, by their presence, divert the metabolic processes and bring about chemical reactions of a different sort."

While the extent of the anthocyan in *O. rubricalyx* proved to be strictly inherited, the various grades of color in *O. rubrinervis*, whose wide range of pigmentation is described and figured in detail, were proved on extensive cultures not to be inherited, the offspring from plants having a relatively low degree of pigmentation having the same average pigmentation as the offspring from parents having a high degree of pigmentation. A strain of oenotheras received from Liverpool, England, which obviously constituted a somewhat heterogeneous population, showed an amount and arrangement of color on the buds similar to those of *O. rubrinervis*, but in this strain the degree of pigmentation was partially hereditary. It seems probable that the apparent inheritance of the degree of pigmentation in the latter case is due to the heterogeneity of the strain, and that the different progenies which resembled their parents in the degree of pigmentation of their buds represent the segregation of more or less pure genotypes from the hybrid mixture.

DEVRIES[8] has continued his studies on hybridization in the oenotheras, and announces results of unusual theoretical interest, which together with the discovery of "twin hybrids," earlier reported[9] by the same author, the reviewer

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[8] DEVRIES, H., Ueber doppeltreziproke Bastarde von *Oenothera biennis* L. und *O. muricata* L. Biol. Centralbl. **31**:97–104. 1911.

[9] ———, On twin hybrids. BOT. GAZETTE **44**:401–407. 1907.

believes will go far toward solving the anomalous hereditary behavior of the oenotheras. As reported in *Die Mutationstheorie* (2:471), reciprocal hybrids among the oenotheras are frequently unlike, being usually similar to the type of the pollen parent. To discover the significance of this phenomenon the author crossed together the reciprocal hybrids, thus $(A\times B)F_1\times(B\times A)F_1$. The results of such a cross he calls "double reciprocal hybrids." For the study of these double reciprocal hybrids he has used chiefly *O. biennis* and *O. muricata*. It will be seen that there are two possible combinations of the same reciprocal hybrids, e.g. (*biennis*×*muricata*)×(*muricata*×*biennis*) and (*muricata*×*biennis*)×(*biennis*×*muricata*). In the first case the *muricata* occupies the middle place in the formula and *biennis* the extremes, while in the second case the position of the two parent species is reversed. The remarkable and unexpected result of these crosses is the complete disappearance of the characters of the species occupying the middle position in these formulae. Thus (*biennis*×*muricata*)×(*muricata*×*biennis*) produces a progeny consisting only of *biennis*, while the alternative arrangement of the parents results in a progeny of pure *O. muricata*, the *biennis* having completely disappeared. This remarkable result does not belong only to the *biennis-muricata* cross, but six other combinations in which *O. biennis* entered as one of the parental types followed always the same law. These six combinations involved a small-flowering "*O. biennis*" from Chicago, *cruciata*, *strigosa*, *Hookeri*, *Lamarckiana laeta*, and *Lamarckiana velutina*. The same principle holds when one of these F_1 hybrids is crossed with one of the parental types, e.g. $(A\times B)F_1\times A$, the result being the same as if the middle parent had not entered into the breeding (in the example the offspring are all pure A). The progeny of such a cross the author calls "sesquireciprocal hybrids."

From these results it is obvious that the eggs and sperms carry different morphological potentialities. The cross A×B results in an AB heterozygote which produces A eggs and B sperms. The reciprocal cross produces only B eggs and A sperms. DeVries offers the explanation that both A and B eggs and A and B sperms are produced, but that the B eggs and A sperms fail, an assumption which is in accord with the observation that about half the ovules and half the pollen grains are abortive.

DeVries has gone further and discovered just what potentialities are carried by each sex. In both pure-bred *O. biennis* and in its crosses with *O. muricata*, the pollen-borne type is epistatic to the seed-borne type, so that the latter is never seen; but in a series of crosses of *O. biennis* with "*biennis* Chicago," *cruciata*, *Hookeri*, *strigosa*, and *Lamarckiana*, the seed-borne type of *O. biennis* is epistatic to the pollen-borne type of the other species, thus allowing it to become visible. The F_1 offspring between *biennis* ♂ and all these other species resemble *O. biennis*, which therefore represents the pollen-borne type. The F_1 between *biennis* ♀ and all of the species mentioned gives a new form unlike *biennis* and unlike any of the pollen parents, but essentially identical in all the crosses. This new form is the seed-borne type of *O. biennis*.

The author calls it the "*conica*-type," because of its characteristic thick conical buds. It has been described already as "*velutina*" in the same author's papers on "twin hybrids." While *O. muricata* was incapable of such complete analysis as was given to *biennis*, owing to the fact that many of its hybrids are weak or sterile, several crosses in which *muricata* was used as the seed parent show that in this species also there is a morphological type determined by the egg cell different from that carried by the pollen cell. The seed-borne type of *O. muricata* is called by DEVRIES the "*frigida*-type." It comes to light in crosses of *O. muricata* as seed-parent with "*biennis* Chicago," *Hookeri*, and *strigosa* pollen parents. It has tall, strong, nearly glabrous stems, but little branched, with flowers resembling *O. biennis*.

These results are of unusual theoretical importance, and the study of double reciprocal hybrids will no doubt lead to the discovery of other instances in which different potentialities are borne by eggs and sperms.

HONING[10] has made a statistical study of the "twin hybrids" of *O. Lamarckiana* and *O. rubrinervis* in the attempt to identify the *velutina* with *rubrinervis* and *laeta* with *Lamarckiana*. He finds in nearly all the morphological characteristics which differentiate the twin hybrids a fairly close parallel with the characters of the mentioned species, and concludes that while they are not identical, *laeta* has a strong predominance of *Lamarckiana* characters, and *velutina* a similarly strong predominance of *rubrinervis* characters. He is convinced by these facts that *O. Lamarckiana* and *O. rubrinervis* are both of hybrid nature, each possessing in the latent state the characters of the other. He offers no suggestion, however, as to how it happens that this hybrid nature fails to express itself when *O. Lamarckiana* and *O. rubrinervis* are self-fertilized.

ZEIJLSTRA[11] has discovered that the most common form of *O. nanella* is parasitized by a *Micrococcus* which forms zoogloea-like masses in the cavities of the cells. The diseased plants have a characteristic appearance which makes them easily detected even in their early stages. Normal (that is, undiseased) *O. nanella* has also been discovered, but much more rarely, and the latter has never fruited. It is suggested that the true normal *O. nanella* may have been frequently overlooked, owing to its resemblance to *O. Lamarckiana*. How it happens that all the offspring of the diseased *O. nanella* are of the parental type needs investigation. The author points out two alternative explanations: namely, that this diseased strain of *O. nanella* inherits a susceptibility to the attack of the *Micrococcus*, or that the germ cells are themselves infected by the parasite. In the latter case a microscopic study of the germ cells should perhaps detect the presence of the *Micrococcus*.—GEO. H. SHULL.

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[10] HONING, J. A., Die Doppelnatur der *Oenothera Lamarckiana*. Zeit. f. Ind. Abstam. Vererb. **4**: 227–278. *figs. 10.* 1911.

[11] ZEIJLSTRA, H. H., *Oenothera nanella* DeVries, eine krankhafte Pflanzenart. Biol. Centralbl. **31**: 129–138. *figs. 5.* 1911.

The determination of sex.—In a recent paper on the determination of sex, STRASBURGER[12] adds to his already extensive contributions to this difficult subject. As in previous papers, he maintains that the problem is phylogenetic, and that there is a striking parallelism between the animal and plant kingdoms in the evolution of sex. In both kingdoms the original differentiation appears only in the haploid generation, but with the differentiation of sex in this generation came fertilization and the formation of a diploid generation, which, in both animals and plants, became the dominant one.

The point at which the separation of sexes takes place in various plant groups is noted briefly; the statements, in most cases, depending upon facts already known, rather than upon cytological or other evidence in connection with this particular paper.

In monoecious Chlorophyceae the thallus is bisexual and the sexes are separated at the formation of oogonia and antheridia; at fertilization the two sexes are united; the reduction of chromosomes takes place during the first two divisions of the zygote, but is not accompanied by any separation of sexes, the product of the zygote being bisexual. In dioecious Chlorophyceae the separation of sexes occurs at the reduction division, so that the products of the zygote are unisexual. Thus the separation of sex tendencies appeared first in connection with the reduction divisions.

In monoecious bryophytes there is no separation of sexes at the reduction divisions, the separation occurring later, at the formation of antheridia and archegonia; but in dioecious forms the separation occurs at the reduction division. That the separation of sex tendencies as well as their union at fertilization is decisive, is shown by the fact that protonema from vegetative cells of a sporophyte of a dioecious moss produces leafy plants bearing both antheridia and archegonia.

In homosporous pteridophytes there is no separation of sexes at the reduction divisions, the spores being bisexual and the sex tendencies being separated later in the gametophytes arising from the spores. The division which many homosporous pteridophytes show in their gametophytes is due merely to external factors, the gametophytes being really monoecious. In heterosporous forms the separation of sexes does not occur at the reduction divisions, but much earlier, during the divisions leading to the formation of spore mother cells, so that the spore mother cells are already all male or all female, all the spores of a microsporangium producing male prothallia and all those of a megasporangium producing female prothallia. The two sex tendencies are united in the sporophyte, which can then produce both microsporangia and megasporangia. Through the heterospory of the sporophyte the dioecism of the gametophyte became firmly established.

In seed plants the sexes are recognized by the external "sex organs" of

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[12] STRASBURGER, EDUARD, Ueber geschlechtbestimmende Ursachen. Jahrb. Wiss. Bot. **48**:427–520. *pls. 9, 10.* 1910.

the diploid sporophyte. In heterosporous plants there is no sex differentiation except that which leads to the formation of microspores and megaspores, for from a microspore mother cell come four spores which produce only male products, and from a megaspore mother cell come four spores which produce only female products. If all sporophytes were bisexual, the problem would be comparatively simple, but there are sporophytes which produce only microsporangia or only megasporangia, and these dioecious seed plants, although their number is comparatively small, have been used extensively in the study of sex problems.

A large amount of experimental work is recorded, the principal forms used being *Mercurialis annua*, *Melandrium rubrum*, and *Elodea canadensis*.

In *Mercurialis annua* ovulate plants sometimes bear occasional staminate flowers, and similarly, staminate plants sometimes bear occasional ovulate flowers. STRASBURGER had already found that the flowers of an ovulate plant, when pollinated from a staminate flower on the same plant, bore seeds which produced only ovulate plants. He now finds that the scattered ovulate flowers on a staminate plant, when pollinated from the same plant, bear seeds which produce only staminate plants. Some plants have ovulate flowers with staminate flowers growing up through them in a sort of proliferation. Pollination of such ovulate flowers with pollen of the proliferating flowers gives rise to seeds which produce both ovulate and staminate plants. The conclusion is that in the scattered staminate flowers the male tendency has become weakened, and that in the scattered ovulate flowers, the female tendency has become weakened.

In the dioecious *Melandrium rubrum*, pollination was effected by pollinating with thin transverse sections of still unopened anthers. It was hoped that in this way pollination would be effected with about equal numbers of pollen grains with the stronger and with the weaker male tendencies. In all, 1475 seeds were secured, and from these there were obtained 1124 seedlings, 1035 of which reached the flowering stage. Of these 376 were staminate and 659 ovulate, the ovulate being strongly dominant.

The work on *Elodea canadensis* is interesting, but is still in an unfinished condition. Although ovulate plants have long been abundant in Europe, staminate plants are not available. Staminate plants and seeds were secured from Wolf Lake, near Chicago, and hundreds of stigmas were pollinated, each with a single pollen tetrad. Fertilization has taken place, but seeds are not yet ripe. If each ovary should produce four seeds, two of which should produce staminate plants and two ovulate plants, there would be some definite data.

The general conclusion from the data, only a small part of which has been indicated here, is that all eggs are female and all pollen male, but that some pollen has a strong and some a weak male tendency. Pollen with a strong male tendency overcomes the female tendency of the egg, while pollen with the weak male tendency is overcome by the stronger female tendency of the egg. The

fact that eggs of apogamous forms may produce staminate as well as ovulate plants does not affect the problem, since such eggs are diploid, and the sex tendencies have not yet been separated. The case is similar to that of budding.

A cytological study was made in *Melandrium rubrum*, *Cannabis sativa*, and *Mercurialis annua*, but at present no cytological features have been recognized which seem to have any bearing upon the problem of the separation of the sexes. In *Melandrium rubrum* one chromosome is constantly larger than the others, as was noted during the reduction divisions and in vegetative cells, but it could not be connected with sex differentiation.

The problem is unusually large and difficult, and the present paper suggests many points of attack.—CHARLES J. CHAMBERLAIN.

Crown gall.—The most noteworthy contribution recently made to plant pathology is the bulletin on crown gall of plants by SMITH, BROWN, and TOWNSEND.[13] This disease, on account of its wide distribution and the conspicuous nature of the deformations to which it owes its name, has long attracted the attention both of practical horticulturists and plant pathologists. Yet, with the exception of the work of some Italian investigators, little has been done to work out the etiology of the disease. From general observations it has been believed that the disease is communicable, and one investigator (CAVARA) isolated an organism from a gall of the European grape and established a strong probability that it was the causal organism of that particular gall. The nature of the outgrowths known as crown gall and occurring on a great many different kinds of plants, the cause of their occurrence, and the relation of the crown galls of different plants to each other, have remained among the most obscure problems in the whole field of plant pathology. The results of investigations on these problems are reported in the present bulletin.

The work begins with a short historical sketch of the more important investigations on the crown gall, special emphasis being laid on the work of Italian investigators who first ascribed the disease to bacteria. This is followed by an account of the isolation of the causal organism, and the evidence showing that the crown gall of various plants is due to bacterial organisms; and that these belong either to a single species or to closely related species or strains, each of which can be inoculated into many species of plants. The morphology and cultural characteristics of the organism (*Bacterium tumefaciens* Smith and Townsend) are described at length. Further, the similarity between crown gall and some animal tumors is discussed. This similarity is emphasized by the occurrence of metastases in infected plants. The last part of the bulletin relates to the practical aspects of the subject, together with a statement of the plants infected and their distribution. The evidence given in the first part is supported by 36 excellent plates.

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[13] SMITH, E. F., BROWN, NELLIE A., TOWNSEND, C. O., Crown gall of plants; its cause and remedy. Bur. Pl. Ind. Bull. **213**: pp. 200. *pls.* 36. *figs.* 3. 1911.

It may be said that the beginning of the present work dates back to the discovery of gall-like outgrowths on the stems of the Paris daisy (*Chrysanthemum frutescens*) in 1904. It was not until 1906, after many unsuccessful trials, that an organism was isolated which when inoculated into sound plants caused the growth of galls similar to the ones from which the organism had been obtained. The organism was inoculated from pure cultures into many different plants, several hundred inoculations having been made. The results showed that on nearly all herbaceous plants tried, such as daisy, pyrethrum, tobacco, clover, cotton, sugar beet, hop, and others, galls were produced as a result of the inoculations. Inoculations into such woody plants as rose, grape, almond, poplar, and Persian walnut also gave galls, but with less frequency than the herbaceous plants. Inoculations on a number of other plants did not result in the formation of galls, although in some instances inoculations had been successful in other experiments with the same plants. Later, crown gall organisms were isolated from a large number of other plants, both woody and herbaceous, including the common nursery trees, as apple, peach, and poplar, which suffer most seriously from the crown gall, and such organisms were also capable of infecting a number of hosts besides the original one. The "hairy root" of apple, which has been more or less associated with crown gall in the minds of nurserymen, was found to be due to the same organism which when inoculated into other plants, as the sugar beet, for instance, gave galls with the characteristic hairy roots. The vast amount of evidence of this nature presented in the bulletin shows that the crown gall and similar tumors, and the hairy root disease of various plants, are due to bacteria, and that the organism of each kind of plant is capable of being inoculated at least into several other plants. The organisms from different sources, while similar in their general characteristics, show minor cultural differences. This behavior leads the authors to leave undecided the question whether the organisms constitute several species or a single species with several races.

An interesting comparison is made between the crown gall outgrowths and animal tumors to which they show resemblance in growth and organization. This resemblance is carried still farther by the formation by the plant galls of metastases, which occur at some distance from the primary gall, but without the intervention of new infections. It is suggested that the metastases occur as a result of growths from the primary galls.

Another important idea is brought out in a number of experiments which tend to show that plants acquire immunity to the crown gall organism as a result of repeated inoculation. If the result of those experiments should be confirmed by future work, this would be the first instance of immunity in plants analogous to that in animals.

This work has removed from the domain of speculation the cause of crown gall and kindred diseases affecting many plants. These diseases, in all their varied manifestations, are shown to be due to a common cause. The enormous

amount of evidence presented leaves no doubt as to the correctness of the conclusions. Aside from having solved one of the most obscure problems of plant pathology, the authors have shown that it has a more general bearing in showing that these plant galls, due to bacteria, present many analogies to animal tumors. The successful isolation of causal bacteria from the plant tumors, after many failures, leads one to hope that the work will stimulate renewed search for organisms in animal tumors.—H. HASSELBRING.

Coastal floras.—H. CHERMEZON[14] has recently made a contribution to the study of coastal floras. In the introduction he calls attention to the well known peculiarity of these floras, the interest they have excited in botanists since ancient times, and the theories advanced as to the relation between them and salt in the soil.

The main part of the work is divided into three sections. In part 1 is given a description of the structure of the leaf and stem of a large number of plants of the coast, chiefly of France, but also of some of the salt-desert regions of Tunis. In part 2 a study is made of the characters peculiar to plants of the coast. There are three categories of habitat: (1) the region of sands, including (*a*) beaches and (*b*) dunes; (2) region of rocks and cliffs, including (*a*) rocks and bowlders exposed to the spray and (*b*) the top of cliffs; (3) damp salty places including (*a*) muddy flats and salt marshes (the halophytic zone par excellence), and (*b*) damp prairies, not reached by the sea, which form a transition to the flora of the interior.

Part 3 is devoted to a discussion of the flora. It is divided into two parts: (1) marshes, rocks, and beaches; and (2) dunes and sands. The transition between the two is made by the plants of the beaches which have characters common to both. In the first group succulency and development of water-tissues are the striking features, while the second shows more often thickening of the cuticle, sinking of stomata, and abundance of hairs. As the stations of the first group are the most salty, while the dunes are not salty at all, the author distinguishes two sorts of floras, the halophilous and the xerophilous. The xerophilous flora reaches its maximum in the dunes, where the characters are such as are met with in other xerophilous floras; but it is less specialized than that of the desert or even the Mediterranean flora, since the dryness is less pronounced and less continuous. The halophilous flora occupies the beaches, the rocks and bowlders, and the salt marshes. The beach and the dunes are not distinct, plants passing from one to the other; but a great many sand-loving plants of the dunes are absent from the beach, which the author explains by the presence of salt, small in amount but sufficient to eliminate them. The rocks and bowlders in the vicinity of the sea, exposed to the spray, are occupied by a flora with special characters, less halophilous than those of

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[14] CHERMEZON, H., Recherches anatomiques sur les plantes littorales. Ann. Sci. Nat. Bot. **12**:117–313. *figs.* 52. 1910.

the beach flora. In the salt marshes is found the most halophytic flora. Several plants have hygrophilous characters, as canals or lacunae.

In conclusion, the coastal flora is composed of xerophilous and halophilous members, showing points of contact; plants of the xerophilous flora have moderately xerophilous characters, such as epidermal protections slightly developed; plants of the halophilous flora exhibit succulency of leaves and of stem and water-tissues; characters in common to the two are isolaterality of leaves and compact structure of the mesophyll.

The author objects to SCHIMPER'S placing halophytes among xerophytes and says: "The assimilation results from confusion between the two different parts of the coastal flora; truly halophilous plants do not often show xerophilous characters; such characters at least in the marshes would be very difficult to explain in spite of the arguments of SCHIMPER; besides, several species of the salt marshes on the contrary have certain hygrophilous peculiarities. The fact that there are succulent plants outside the coast simply proves that succulency may be related to other factors of the soil besides salt, but its frequency in plants of salty earths shows that there exists a certain relation between succulency and salt. The nature of the relation is impossible of determination." Either argument, that succulency permits plants to resist the toxic action of salt, or that the appearance of succulent plants on the coast is due to lack of competition there, he thinks insufficient, and concludes that a flora as special as that of the salt marsh should be considered as halophilous in the proper sense of the word. The author admits that succulency may be due to other factors than salt in the soil, but does not make it clear why he objects to considering that "physiologically dry" soil and really dry soil may occasion the same structure. SCHIMPER'S argument seems to us to stand. —A. M. STARR.

Inheritance of flower-form and color in Digitalis.—A familiar garden variety of *Digitalis* has the central axis terminated by a peloric flower. KEEBLE, PELLEW, and JONES[15] find that this form is a Mendelian recessive to the typical form, and that, as might be expected, the inheritance is the same whether the seeds are taken from the peloric flower or the normal zygomorphic flowers of the same plant. The flower-color is referred to three pairs of allelomorphs: *Mm*, a magenta factor; *Dd*, a darkener which changes the magenta to purple; and *Ww*, a dominant white factor which removes the effect of *M* except in the small spots which occur on the corollas of all *Digitalis*. When *M* is present these spots are red, and when absent they are yellow.

MISS SAUNDERS[16] has studied the inheritance of an interesting form of

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[15] KEEBLE, F., PELLEW, MISS C., and JONES, W. N., The inheritance of peloria and flower-color in foxglove (*Digitalis purpurea*). New Phytologist **9**:68–77. *fig. 1.* 1910.

[16] SAUNDERS, MISS E. R., On inheritance of a mutation in the common foxglove (*Digitalis purpurea*). New Phytologist **10**:47–63. *pl. 1. figs. 12.* 1911.

Digitalis which has been noted occasionally for nearly a century, and which was described by CHAMISSO in 1826 under the name *D. purpurea heptandra*. The characteristic features of this form consist of a dialysis of the corolla and staminody of three or more of the petals, thus producing flowers having most typically 7–9 stamens, and scarcely to be recognized as a *Digitalis* flower at all. The degree of development of these characters is variable, and somewhat influenced by the environment, but there is no real transition to the normal form. This form proves to be like the peloric variety, a Mendelian recessive to the normal. The reviewer has also been studying the inheritance of this peculiar variety for five years, and has reached the same conclusion. Miss SAUNDERS confirms the results of KEEBLE, PELLEW, and JONES as to the color-characters.—GEO. H. SHULL.

Water relations of desert plants.—FITTING[17] has studied the water relations of the plants growing on the Sahara. He finds, as LIVINGSTON found for the Arizona desert, that the water is generally gained from the surface layers of the soil and not by deep rooting. Many of the plants, especially the perennial shrubs not provided with water-storage organs, develop remarkably high osmotic pressure, which enables them to withdraw water from the comparatively dry soil. On the other hand, the annuals showed much lower osmotic pressure, with lack of ability to thrive in the most exposed places. In many cases the high pressures were due largely to stored NaCl, but frequently entirely to other solutes. Of the 46 species studied, 21 per cent showed an osmotic pressure exceeding 100 atmospheres; 35 per cent exceeded 53 atmospheres; 52 per cent, 37 atmospheres; while only 11 per cent showed osmotic pressures as low as 11 to 22 atmospheres. Species showing extremely high pressures in dry desert conditions show much lower pressures in moist situations. This marked power of certain plants to adjust their osmotic pressures to the water-withholding power of the medium in which they grow has been demonstrated for salt marsh plants by HILL,[18] a piece of work which FITTING does not cite. We have known little about the osmotic pressure of desert forms, and this work supplies much of the deficiency and makes this character of great significance in the physiology of these forms.—WILLIAM CROCKER.

Permeability.—SCHROEDER[19] has studied the semipermeable membrane of the wheat grain, and confirms the work of BROWN on the barley, but adds little that is new. The portion of the coat forming the semipermeable mem-

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[17] FITTING, HANS, Die Wasserversorgung und die osmotischen Druckverhältnisse der Wüstenpflanzen. Zeitsch. Bot. **3**:209–275. 1911.

[18] HILL, F. G., New Phytologist **7**:133–142. 1908; Rev. in BOT. GAZETTE **47**:170. 1909.

[19] SCHROEDER, H., Ueber die selektiv permeable Hülle des Weizenkornes. Flora **102**:186–208. 1911.

brane originates either from the inner integument or from the nucellus. The following substances dissolved in water cannot pass through the membrane: NaF, KCl, KNO_3, K_2CO_3, Na_2CO_3, $BaCl_2$, Na_2SO_4, $MgSO_4$, $AgNO_3$, $COCl_2$, and sucrose; while $HgCl_2$, iodine, methyl and ethyl alcohols, ethyl ether, acetone, acetonitril, and chloroform with water as a solvent will enter. In dead grains the membrane still retains its semipermeable character. It is shown that water and the solutes capable of entering do so mainly through the embryo end of the grain. The membrane becomes permeable to $AgNO_3$ if alcohol is added to its water solution. Ether renders the coat more readily permeable to water, while treatment with osmic acid renders it less so. While this membrane, being of the non-protoplasmic type, is of great theoretical interest, it has not been demonstrated of any biological significance to the seed itself. In these cultivated forms it is probable that, if such a significance existed, it has been eliminated by selection. A study of this membrane in wild grasses might prove of interest. Many of the wild forms show delayed germination, and in one at least, wild oats, rupturing the coat overcomes the delay.—WILLIAM CROCKER.

Leaf-fall.—The phenomena accompanying the process of defoliation have been investigated by LEE[20] in nearly 50 species of trees and woody plants. The separation layer is formed from existing cells, with or without division, and cuts off the leaf by the degeneration and disappearance of the middle lamellae of the cells involved. The vascular elements are ruptured, but usually only after tyloses have filled them. The character of the invariably present protective layer is made the basis of classification, and the species studied are segregated according to whether the ligno-suberized protective cells arise (1) without further modification from existing cells; (2) after irregular division of existing cells; or (3) from a regularly active cambium. Whether the ligno-suberization comes before or after defoliation leads to subdivisions of the first two classes. The production of a cork layer continuous with the periderm of the stem usually follows in the growing season succeeding defoliation.—GEO. D. FULLER.

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[20] LEE, E., The morphology of leaf-fall. Annals of Botany **25**:51–106. 1911.

Vol. LII No. 2

THE BOTANICAL GAZETTE

August 1911

Editor: JOHN M. COULTER

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VOLUME LII NUMBER 2

THE
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AUGUST 1911

THE ADULT CYCAD TRUNK

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 146

CHARLES J. CHAMBERLAIN

(WITH TWENTY FIGURES)

The structure and development of the cycad seedling is fairly well known in all the genera, and in *Dioon*, *Ceratozamia*, and *Microcycas* recent investigations have been particularly thorough; but some features of the adult trunk have hitherto escaped observation, doubtless because such material is so difficult to obtain. As a matter of fact, most of the descriptions are based upon dead conservatory plants which had begun to decay and so had become worthless as ornamental specimens.

Historical

As early as 1829, BRONGNIART (1) described the stem of *Cycas revoluta*, and showed clearly that, in spite of the external habit, the woody structure was not at all related to that of palms, but resembled the wood of dicotyls, the principal difference being that *Cycas* had no bast or growth rings.

VON MOHL (2) studied a specimen of "*Zamia latifolia*" (*Encephalartos*) 1.5 meters in height, and also a section of a large trunk of *Cycas revoluta*. He recognized the bast and described the histological characters of the wood, which he found to resemble that of dicotyls, except that it lacked true vessels. In the pith he found bundles like those of many cacti. There were no growth rings.

The excellent work of METTENIUS (3), published in 1861, deals with *Cycas revoluta*, *Encephalartos horridus*, *Dioon edule*, and *Zamia muricata*. The course and structure of leaf traces are described in detail, and spiral vessels are noted for the first time, these having escaped the observation of previous investigators, probably because in mature stems they are lacking next the pith, where one might expect to find them. He saw bundles in the pith of *Dioon* and correctly interpreted them as belonging to the vascular system of the peduncle.

SOLMS-LAUBACH (4) traced the vascular supply of the peduncles in *Stangeria paradoxa* and *Ceratozamia mexicana*, and also noted the formation of phellogen in the leaf bases.

In his *Histologische Beiträge* III, STRASBURGER (5) describes the histological structure of a large trunk of *Cycas circinalis*, and gives a critical discussion of the literature.

In 1896, WORSDELL (6) made a thorough investigation of a large trunk of *Macrozamia Fraseri*. This form has a well-developed system of vascular bundles in the pith, described as not being connected in any way with peduncles. There are also concentric zones of wood, as in *Cycas*, and these, WORSDELL (6) believes, are remnants of some ancient structure which consisted of rings or layers of concentric vascular strands. To him the structure recalls that of the *Medullosa* stem.

From these accounts we get our conventional idea of the cycad stem, with its armor of leaf bases, thick cortex, narrow zone of wood, large pith, numerous medullary rays, and no growth rings.

Investigation

In September 1910 I was able to study in the field the adult trunks of *Dioon edule* and *D. spinulosum*, the study being facilitated by the active encouragement of Gov. TEODORO A. DEHESA, of the state of Vera Cruz. The field study was supplemented by notes and material from Mr. ALEXANDER M. GAW, of the Bureau of Information, Jalapa, state of Vera Cruz. Abundant material of *Dioon spinulosum*, accompanied by notes, was sent to me by Mr. J. C. DENNIS, superintendent of the Hacienda de Joliet, near Tierra Blanca, but in the state of Oaxaca. I am glad to acknowledge my

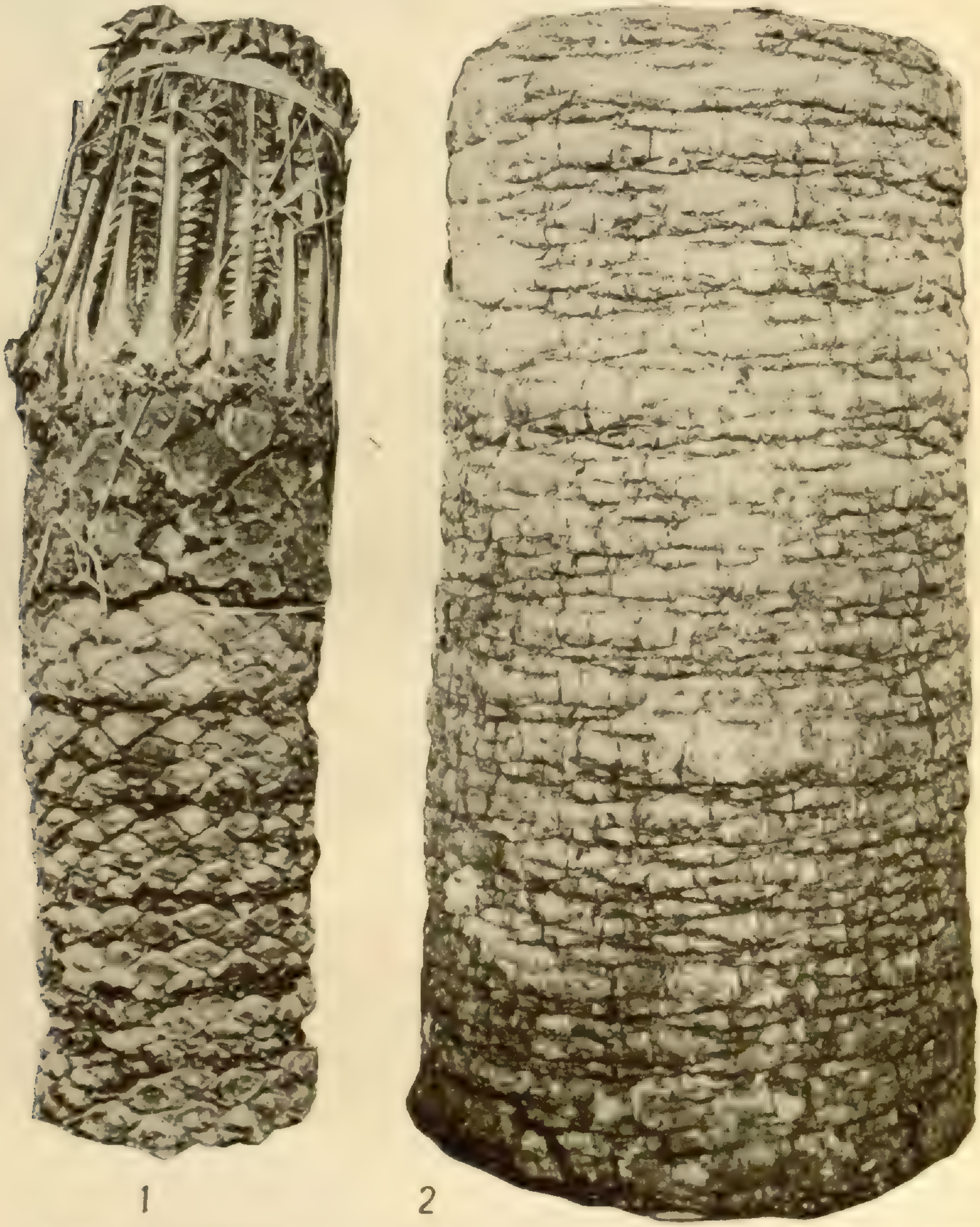
indebtedness to these gentlemen, for without their cooperation the investigation of such inaccessible material would have been impossible.

MACROSCOPIC STRUCTURE

The conventional account of the trunk is doubtless true for all young cycads and for most old ones, but it is not correct for large plants of *Dioon spinulosum*, and probably not for others which have attained any considerable height. In *D. spinulosum* the large amount of wood, the zone sometimes reaching a thickness of 10 cm., first attracted my attention, but since material was available, it seemed desirable to examine the whole trunk. Plants were studied both at Tuxtepec and at the Hacienda de Joliet, but the following account, whenever it relates to *D. spinulosum*, is based upon material from the latter locality.

AGE.—As mentioned in a previous paper (**7**), the trunk sometimes reaches a height of more than 16 meters. From the crown to the base the trunk is marked with a series of ribs due to the alternation of foliage and scale leaves, the constrictions between ribs corresponding to the scale leaves, and the ribs themselves being the larger leaf bases of the crowns of foliage leaves. Obviously, the number of crowns which a plant has borne can be determined by counting the ribs, and, assuming that a new crown is produced each year, the age of the plant would then be known. But it is not certain that new crowns are formed every year, and whether the interval is regularly two years remains to be determined. At any rate, an estimate making the number of years correspond to the number of crowns would be extremely conservative. In our previous account (**7**) the age of the tallest specimens was estimated at about 400 years, the estimate assuming a crown to be produced every other year. It was also stated that the scars are so obscure on the lower portions of the trunk that accurate counting is difficult. While this is true, we now find that the counting can be carried much farther than we had supposed, and also that the obscure ribs formed by successive crowns are very much closer together in the lower than in the upper portion of the trunk. The difference between the upper and lower portions of a trunk 6 meters in height is shown in figs. 1 and 2, the lower portion being taken

30 cm. above the surface of the rock upon which the plant was growing. The foliage display practically always consists of two successive crowns, the leaves of the lower standing transversely or beginning to droop, while those of the latest crown are more erect, but the two nevertheless presenting the appearance of a single



FIGS. 1, 2.—*Dioon spinulosum:* fig. 1, upper part of a trunk 6 meters in height; the latest crown is tied with the string, the next crown below has been cut away with a machete, and the leaves of the 6 crowns below this have fallen off naturally; $\times\frac{1}{6}$; fig. 2, lower part of same trunk, showing scars of 21 crowns; $\times\frac{1}{5}$.

crown. In fig. 1 the latest crown is tied to protect the bud, and the leaves of the crown below have been cut off. With this explanation, it will be seen that the upper portion has borne 8 crowns. The lower portion has borne 21 crowns, of which 6 or 7 toward the top are easily counted, while the rest are increasingly indistinct. How many crowns were borne by the intervening piece, about 4 meters in length, and also by the stump, is not known, but 100 crowns would be a very low estimate, and the plant would be more than 100 years old even if a new crown were produced every year.

ARMOR.—In some forms, like *Dioon edule* and *Encephalartos Altensteinii*, the armor of leaf bases is so persistent that each leaf base is distinguishable even in the lower portion of the trunk, while in *Dioon spinulosum* and others the leaf bases become indistinguishable in the lower portion of old trunks.

In *Dioon edule*, below the two green crowns constituting the foliage display and appearing as a single crown, is a crown represented by decaying midribs from which most of the leaflets have fallen, and below this will be found one or more crowns represented by irregular jagged stumps, several centimeters in length, and it is only below these that one finds the smoothly cut off bases. The reason is easily determined. As in annually deciduous dicotyls, an abscission layer of phellogen is developed, but at so late a period that only a decayed stump of midrib remains to be cut off. After the stump has fallen, a new phellogen appears a little deeper than the first, and then another, so that successive phellogens keep scaling off the outer surface, even in forms with such persistent leaf bases as *Dioon edule*. At Chavarrillo, where this species is most abundant, the trunk is often damaged by fire. In such cases, where the entire armor may be destroyed, an extensive phellogen appears in the cortex, the meristematic layer sometimes reaching a width of several millimeters, and in this way a smooth protective covering is built up.

In *Dioon spinulosum* the phellogens are more vigorous, and successive layers are scaled off until the leaf bases in the lower portion of old trunks become indistinguishable, and even the ribs due to the alternation of scale and foliage leaves become obscure. We have

never seen a specimen of *Dioon* from which all of the armor had scaled off, except in case of injury.

CORTEX.—The cortex of a large plant grows rapidly for a few years, and then during the long life of the plant grows very little. In a 6-meter specimen of *Dioon spinulosum*, at a distance of 15 cm. below the apex, the width of the zone of cortex, measured from the outer border of the phloem to the beginning of the leaf base region, was 1–1.5 cm.; while the width of the cortex near the base of the stem, where the tissues were at least 100 years older, had increased only to 1.5 or 2 cm.

Except in cases of injury, there are no meristematic regions in the cortex, *Dioon* being strictly monoxylic, and there is no growth by a phellogen at the periphery, the phellogen layers being confined to the leaf base region and not reaching the cortex itself. In forms which lose their armor through the vigorous activity of successive phellogens, the cortex itself is invaded, but in such cases the invading phellogen adds as much or more than it cuts off, and the stem may even increase in diameter.

The cortex is traversed by numerous leaf traces, some of them direct and others forming the characteristic girdle. There are also numerous mucilage canals and cavities, some of them following the course of the bundles, but most of them being independent. Crystals of calcium oxalate are numerous, and tannin cells are so abundant that a freshly cut stem changes color in a few minutes.

AMOUNT OF XYLEM.—The cycad stem has always been described as having a large pith and cortex, with a small zone of wood between them.

According to BRONGNIART (1), a specimen of *Zamia latifolia* (doubtless an *Encephalartos*), 1.5 meters in height and 20.5 cm. in diameter, had a pith 7.5 cm. in diameter, surrounded by a vascular zone 6 mm. in width, the xylem and phloem being of about equal thickness; beyond the phloem was a narrow cortex about 8 mm. in width, followed by a broad zone of leaf bases 5 cm. in width.

A few measurements which we have made recently are given below, all measurements being made at approximately the greatest diameter of the plant.

A plant of *Ceratozamia mexicana*, collected about 10 kilometers north of Jalapa, had a trunk 30 cm. high and 15 cm. in diameter. The pith, 5.7 cm. in diameter, was surrounded by a zone of zylem 3 mm. wide, with phloem 2 mm. wide, beyond which was the cortex 1.5 cm. wide, and surrounded by a heavy armor of leaf bases.

A mature plant of *Zamia floridana*, with a stem 15 cm. in height and 6 cm. in diameter, had a pith 1.3 cm. in diameter, the zones of xylem and phloem each measuring 2 mm. in width, and the cortex about 2 cm. in width. The entire armor had disappeared, and a comparatively regular phellogen had become established in the cortex.

A specimen of *Dioon edule* at Chavarrillo, with a trunk about 60 cm. in height and 21 cm. in diameter, had a pith 8.7 cm. in diameter, the zones of xylem and phloem each measuring 5 mm. in width, the cortex 2 cm., and the leaf bases 3.6 cm. A taller specimen, about 1 meter in height, but with the same diameter, had the following dimensions: diameter of pith, 6.9 cm.; width of xylem, 1.5 cm.; width of phloem, 8 mm.; width of cortex, 3.2 cm.; width of leaf base region, about 1.5 cm.

These measurements may be regarded as typical of most monoxylic trunks. The mount of wood in polyxylic trunks, though somewhat greater, is still so scanty that no exception to the conventional description has been necessary.

Naturally, it was with considerable surprise that I noted, in the Tierra Blanca region, trunks of *Dioon spinulosum* with zones of wood 4, 6, and even 10 cm. in width. A specimen 6 meters in height, and 33 cm. in diameter at a distance of 30 cm. above the rock on which it was growing, had a zone of wood 10 cm. in width. The phloem was 1.4 cm. in width, the cortex 2.5 cm., and the armor near the base of the plant, where it had been greatly reduced, only 0.5 to 1 cm. The pith at a distance of 60 cm. below the apex was 8 cm. in diameter, and from this point to the base of the plant its diameter was uniform. What the extent of the wood in a specimen 15 or 16 meters in height might be, remains to be determined.

The numerous large medullary rays reaching from the pith to the cortex are a conspicuous feature of the transverse section (fig. 3). Besides the large rays there are much more numerous small

ones. Both kinds of rays have a comparatively slight longitudinal extent. Each large medullary ray contains a leaf trace bundle, but the small rays are in no way connected with bundles.

GROWTH RINGS.—*Dioon spinulosum* has well-developed growth rings, a feature which, so far as I know, has not been described for any cycad. These rings are conspicuous in the upper part of the trunk, and can be recognized even in the lower portions of old plants (figs. 3 and 19). That the rings are growth rings, and that

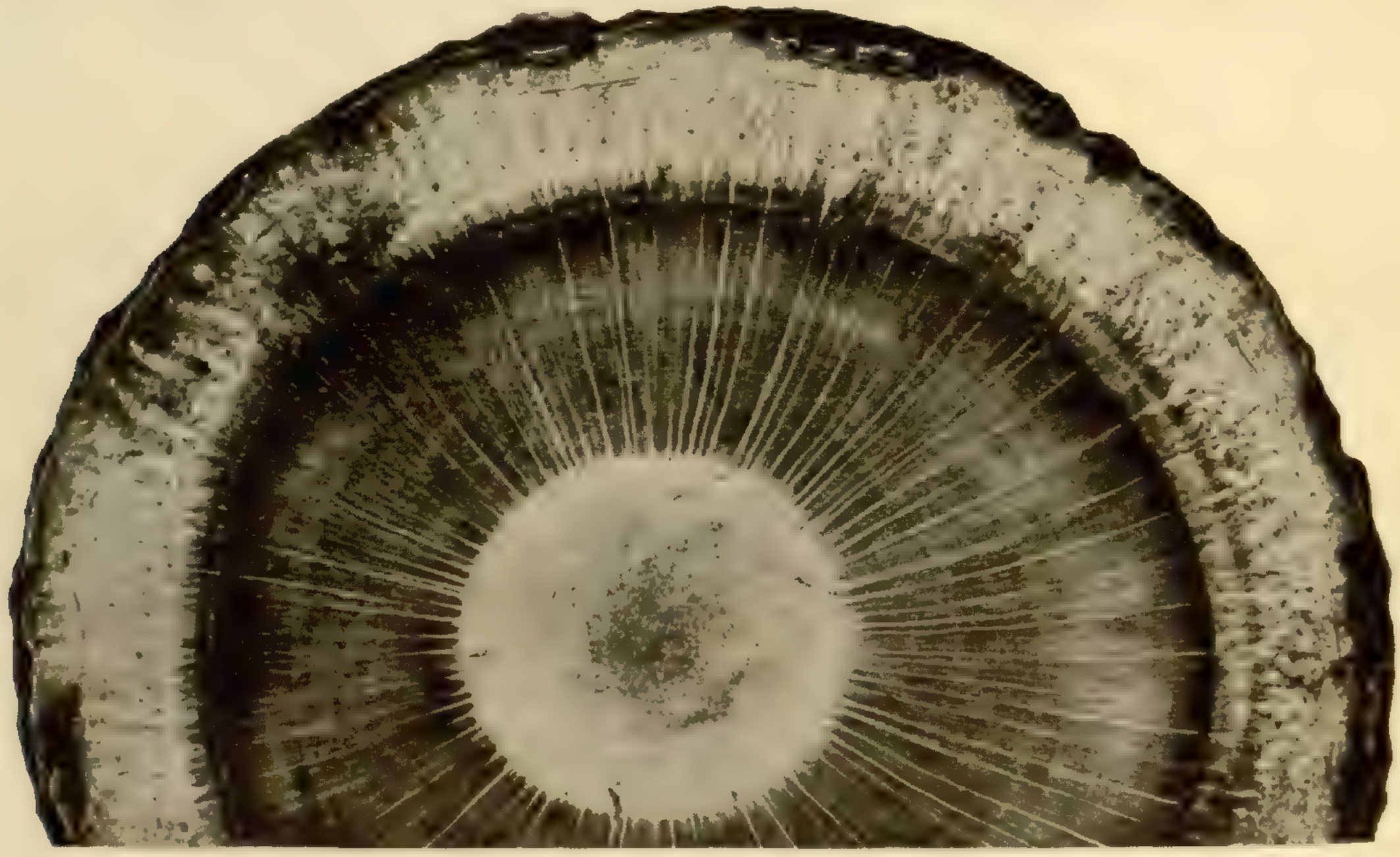


FIG. 3.—*Dioon spinulosum:* transverse section of lower part of the piece shown in fig. 2; note the large and small medullary rays, the growth rings, and the large amount of phloem; $\times\frac{1}{3}$.

they have approximately the same structure as the annual rings of dicotyls, is obvious from a glance at a transverse section; but that they are annual rings is doubtful even in *Dioon spinulosum;* and in *D. edule,* where the rings are equally conspicuous, it is absolutely certain that they are not formed annually.

A transverse section of the 6-meter plant of *Dioon spinulosum,* already mentioned, at the level of the third crown from the apex, showed four growth rings. This piece had borne one cone. A section of the same plant at the level of the eighth crown below the apex showed 13 growth rings. During the formation of the nine crowns the plant had produced at least 8 cones.

The number of rings, counted 30 cm. above the ground in the 6-meter specimen, was about 150. The number of crowns, at a very low estimate, was about 100. Any estimate of the number of cones would necessarily be very uncertain, the only data being that the first cone was borne when the plant was 1 meter in height, and that a piece 25 cm. in length, taken near the top of the plant, had borne 6 cones. Estimated only upon this data, the number of cones would have been more than 100, but the estimate is doubtless much too high, because ovulate cones are comparatively infrequent on small plants.

The number of rings, then, does not correspond exactly to either the number of crowns or the number of cones, or to the number of both combined. It is certain that in some seasons a plant produces a crown of leaves but no cone; and that it may produce a cone and no leaves; and, further, that it may produce both a new crown and a cone the same season, or it may fail to produce either a crown or a cone. It is quite probable that when either a crown or a cone is produced, a ring is formed, and that when both a crown and a cone are formed the same season, only one ring is produced.

We are inclined to believe that a period of vigorous growth, which would result in the formation of a new crown or cone, would produce also a growth ring, and that seasons which pass without the formation of a crown or a cone would not be marked by growth rings, the mere alternation of rainy and dry seasons not being sufficient for the formation of a ring in *Dioon*. If the number of rings should correspond somewhat approximately to the number of seasons, we should regard the correspondence as a coincidence, the crown and cone production being the determining factor. Of course, it is well known that dicotyls in such localities have seasonal growth rings.

In *Dioon edule* the growth rings present a very different problem, for it is certain that they correspond to neither the number of crowns, number of cones, nor number of seasons. At Chavarrillo, a plant 60 cm. in height and 20 cm. in diameter showed, in a transverse section near the base, a zone of wood 15 mm. in width. The number of rings was about 20, but the age of the plant, at a very conservative estimate, could not have been less than 100 years,

nor the number of crowns less than 50, so that whatever the factor may be which produces the ring, it must appear at widely separated intervals. The trunk is obscurely ribbed, but the ribs do not correspond to the number of crowns, many crowns being represented in each rib. It is possible that these ribs are due to the resting periods during which neither crowns nor cones are produced. The number of rings may correspond to the number of these resting periods. It is possible that such resting periods may result in the formation of new zones of wood in polyxylic stems, like *Cycas revoluta*, and only in the formation of rings in *Dioon edule*. In either case, it would require time and some vandalism to secure evidence.

CONE DOMES.—Vascular bundles in the pith have doubtless been seen by everyone who has cut a section of any mature cycad stem, but METTENIUS (**3**), studying *Dioon edule*, was the first to interpret these bundles as the vascular system of the cones. Later, SOLMS-LAUBACH (**4**) made a more thorough study of the pith bundles in *Ceratozamia*, and showed conclusively that the cycad trunk is a sympodium. Still later, the mode of development of the sympodium was described by Miss F. GRACE SMITH (**8**), who studied the origin of young cones and stem apices in *Zamia floridana*.

We have studied the pith bundles in *Dioon spinulosum*, *D. edule*, and *Zamia floridana*. In longitudinal sections of the stem, the bundles are in the form of a convex diaphragm, but since they really form a dome with the peduncle of the cone at its apex, we shall call the system of bundles a *cone dome*.

The longitudinal section shown in fig. 4 contains five cone domes, the second of which, counting from the top, is cut through the axis of the peduncle, and the third and fifth show clearly the position of the peduncle, and the other two indicate its approximate location by a thickening of the bundles. In *Zamia floridana* the appearance is similar, but in *Dioon edule*, on account of the very slow growth, a single transverse section may show parts of as many as three cone domes.

In transverse section the cone dome appears as a circle of vascular bundles more or less eccentric if cut near the peduncle, but concentric near the stele (fig. 5).

As soon as a cone begins to develop, a new meristem appears very close to the peduncle, and this new meristem may form successive crowns of leaves, but sooner or later it becomes transformed into a cone, which is really only a highly modified crown of leaves

FIG. 4.—*Dioon spinulosum:* longitudinal section near the top of the piece shown in fig. 1; note 5 cone domes and, at the tip, a part of another; three ribs and parts of two more are shown; between the ribs are scale leaves; ×½.

terminating the growth of its axis. The process is then repeated. An instructive view of this phase is seen in fig. 6. A little to the right of the center is the peduncle of a large ovulate cone, and at its left is the new growing point which has produced a crown of foliage

eaves, and a crown of scale leaves appearing as a whitish triangular cluster in the figure, while the growing point itself is becoming transformed into a cone, a fact evidenced, as yet, only by a slight elongation, the point, while producing only vegetative leaves,

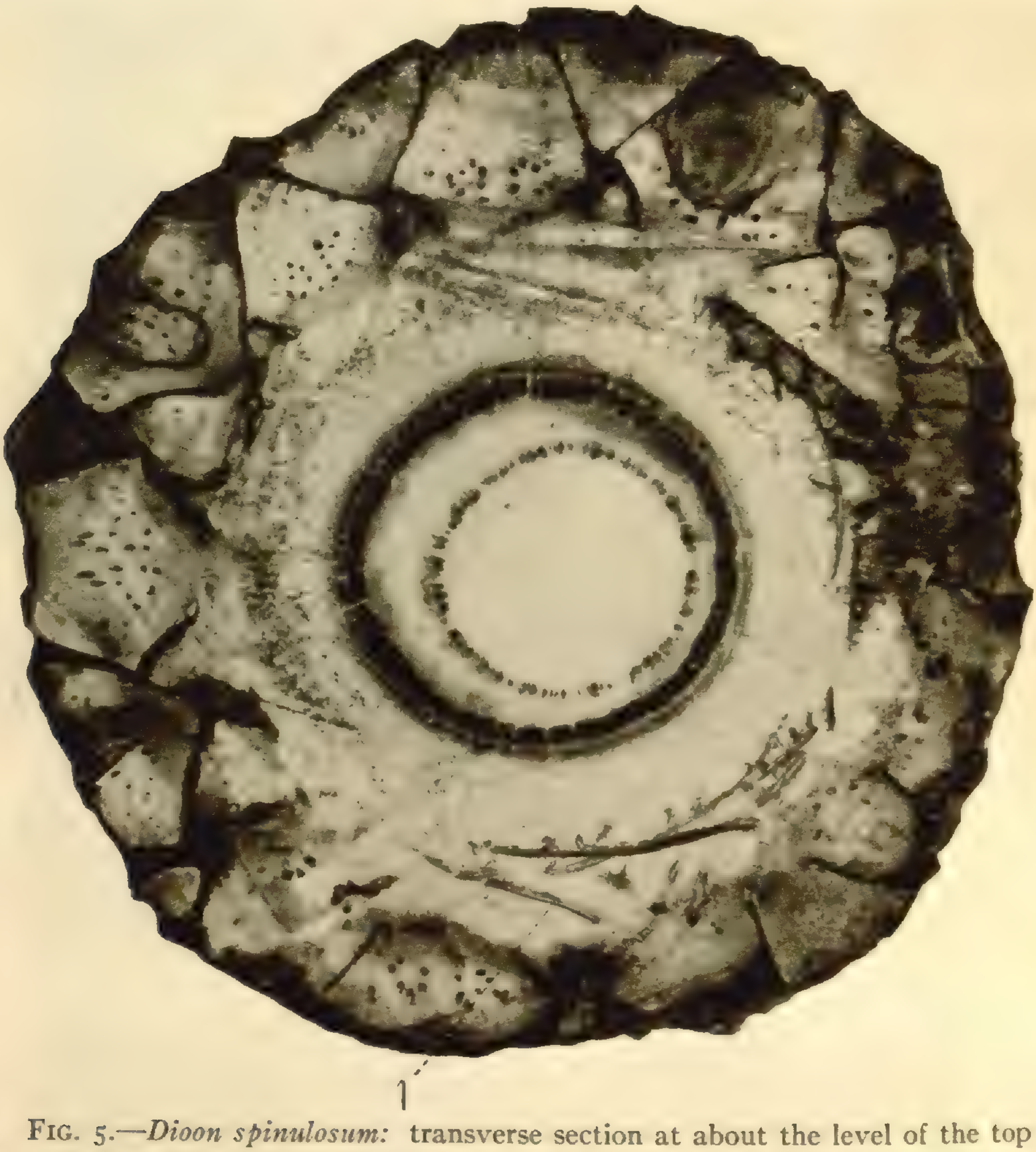


FIG. 5.—*Dioon spinulosum:* transverse section at about the level of the top of fig. 4; the innermost ring is the cone dome; beyond this is the vascular cylinder, with the xylem (quite dark) and the phloem (much lighter) about equal in width; the girdle leaf traces (*l*) are prominent; ×½.

being convex or at most hemispherical. Young cones of *Zamia* also may be distinguished from vegetative growing points, even before any appearance of sporophylls, by the elongation.

As the new apex develops, the old peduncle is pushed aside, new tissue gradually surrounds its base, and finally whatever

remains of the old peduncle is covered over, somewhat as in the case of a dead branch of a dicotyl. The apex of the cycad stem is remarkably broad and flat, a feature which expedites the burying of the peduncle by the new tissue (fig. 6).

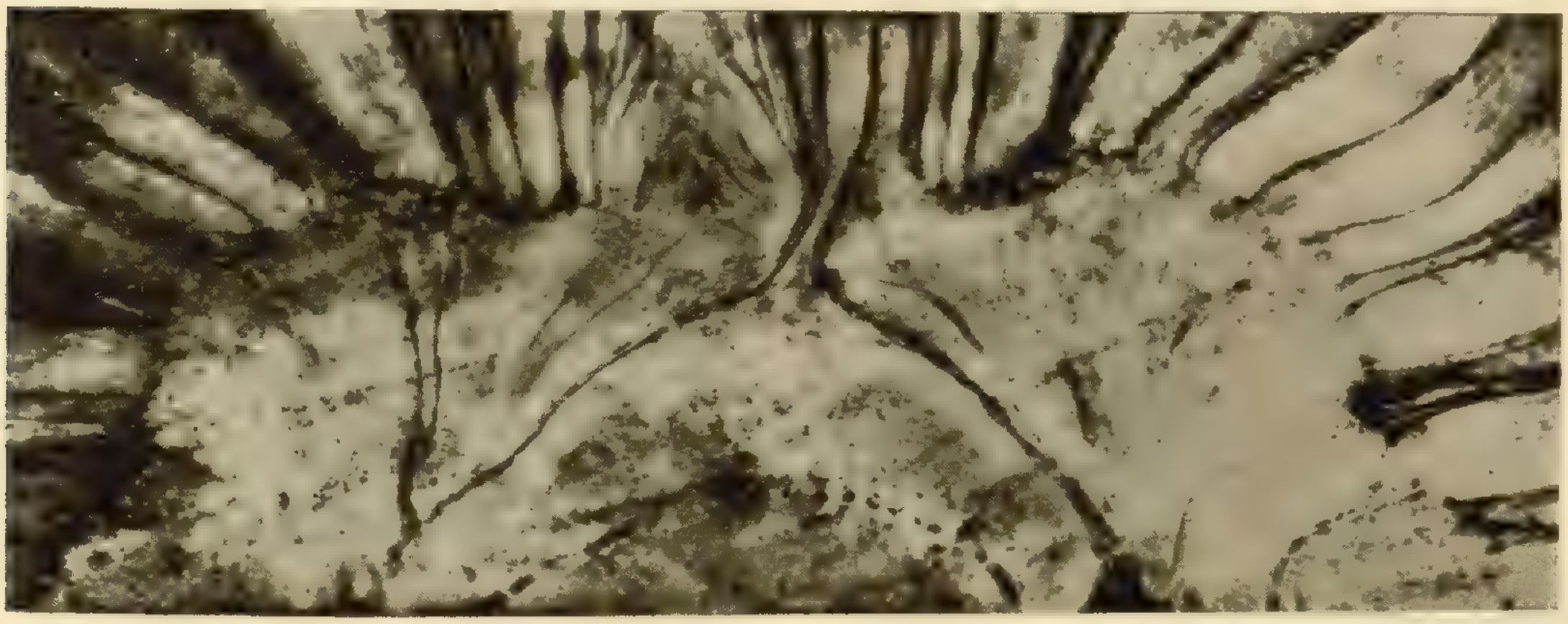


FIG. 6.—*Dioon edule:* longitudinal section of the apex of a large trunk, showing three cone domes, the lowest with bundles in transverse section, the middle one with bundles going to the peduncle of a large cone, and the upper terminating in the latest apex; $\times\frac{2}{3}$.

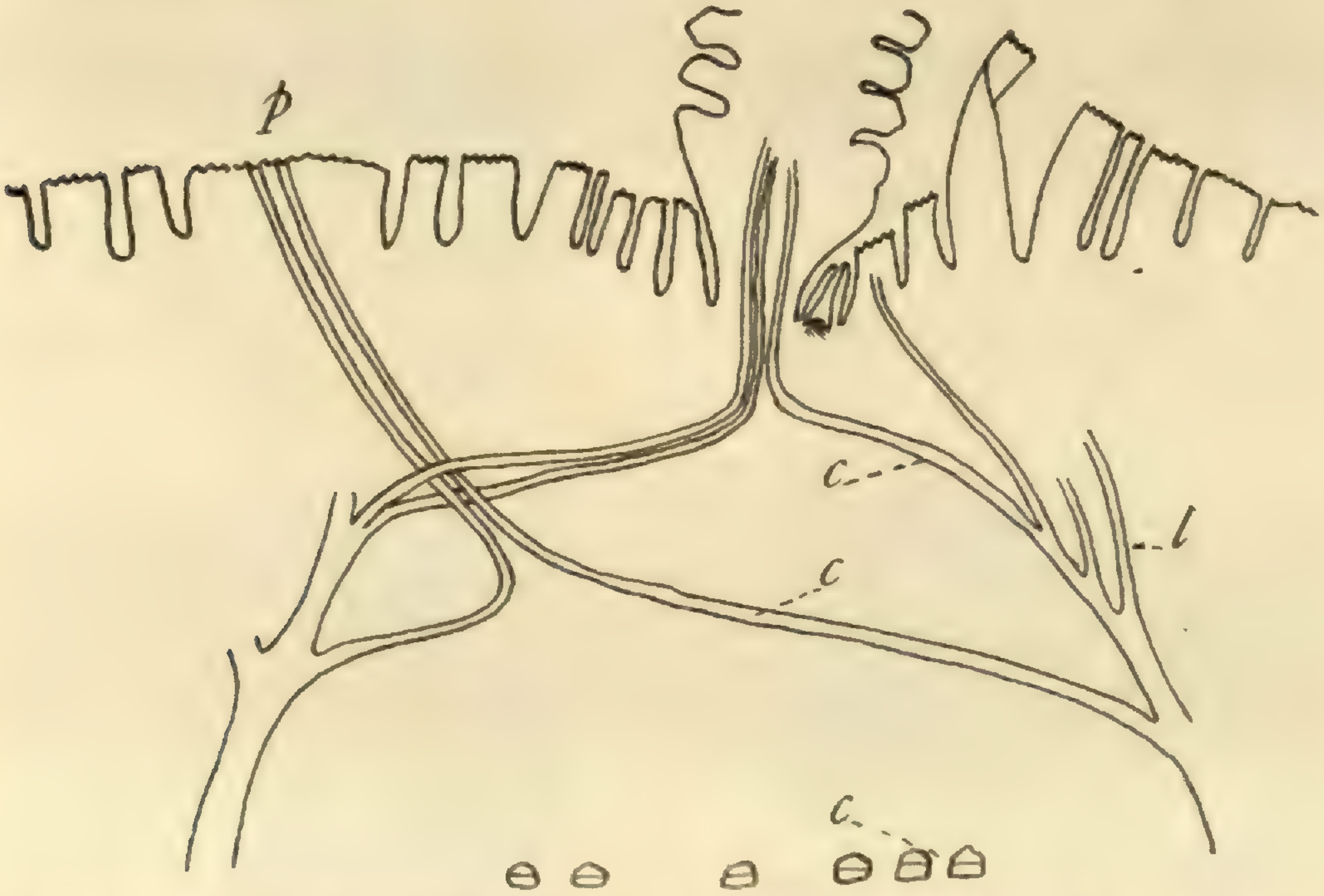
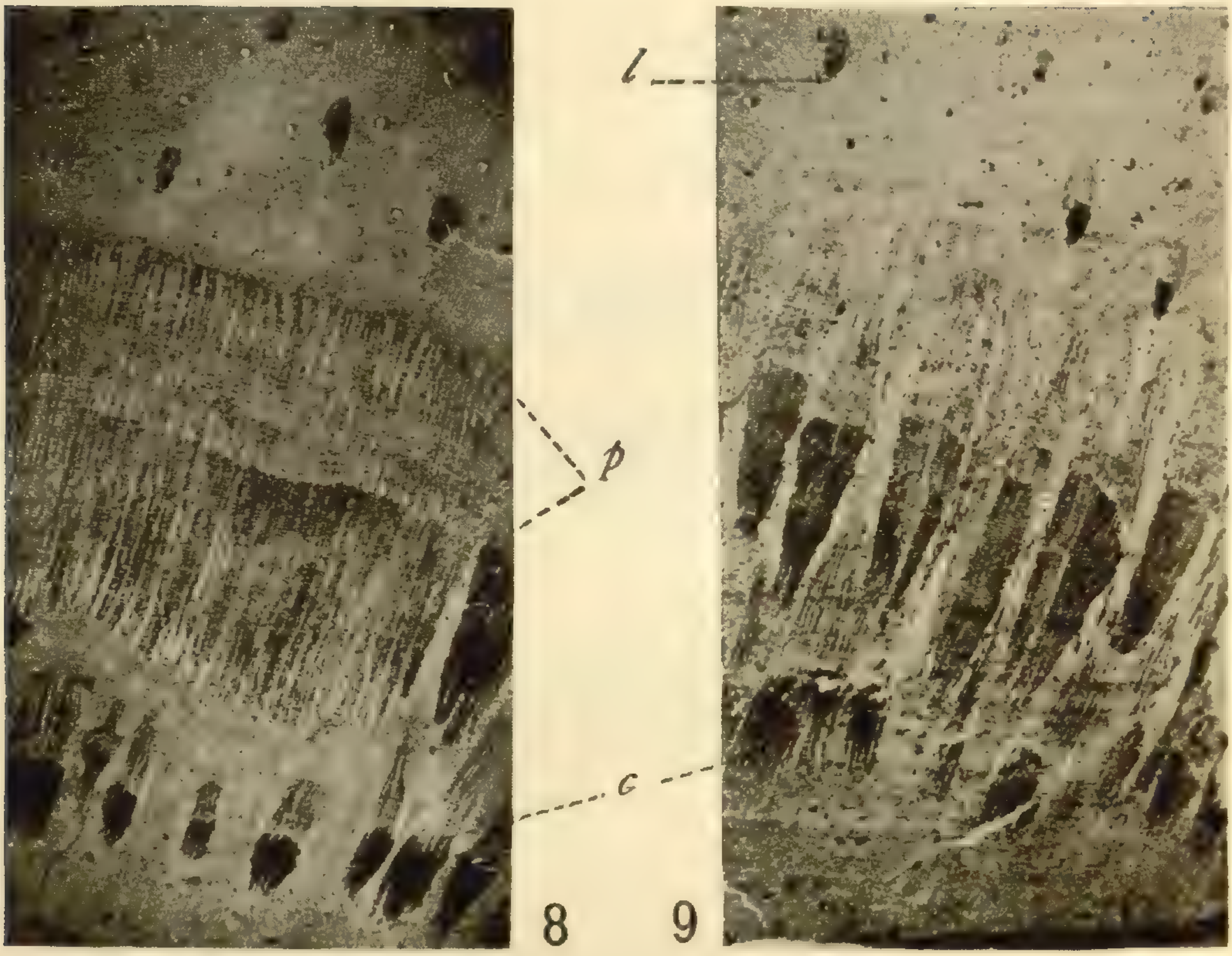
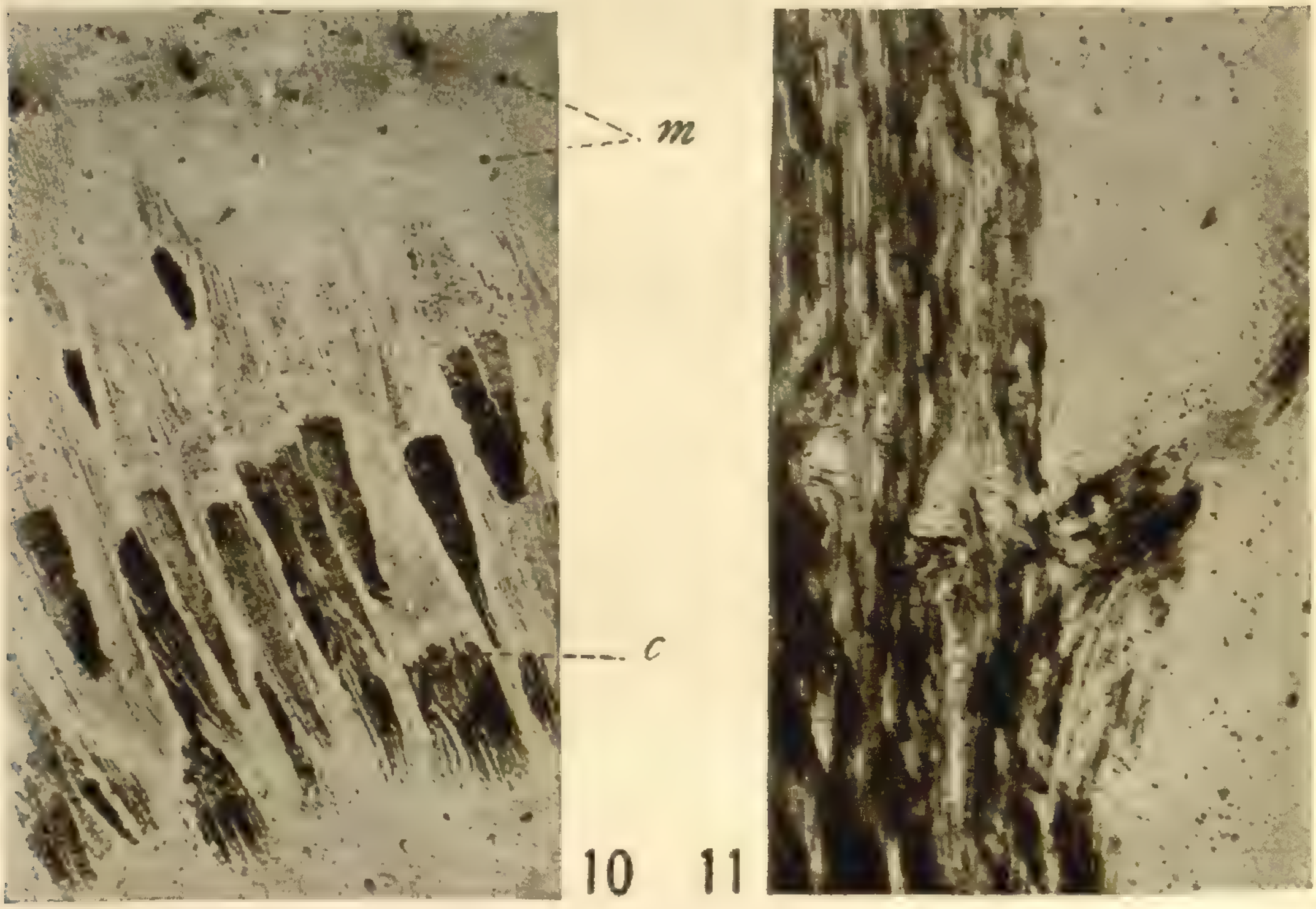


FIG. 7.—*Zamia floridana:* longitudinal section of apex of a large plant, showing three cone domes (*c*), the lower with bundles in transverse section, the middle with bundles running to the peduncle (*p*) of a mature cone, and the upper with bundles running to a young cone; the new growing point is at the right of the young cone; several leaf traces (*l*) are shown; $\times 3$.





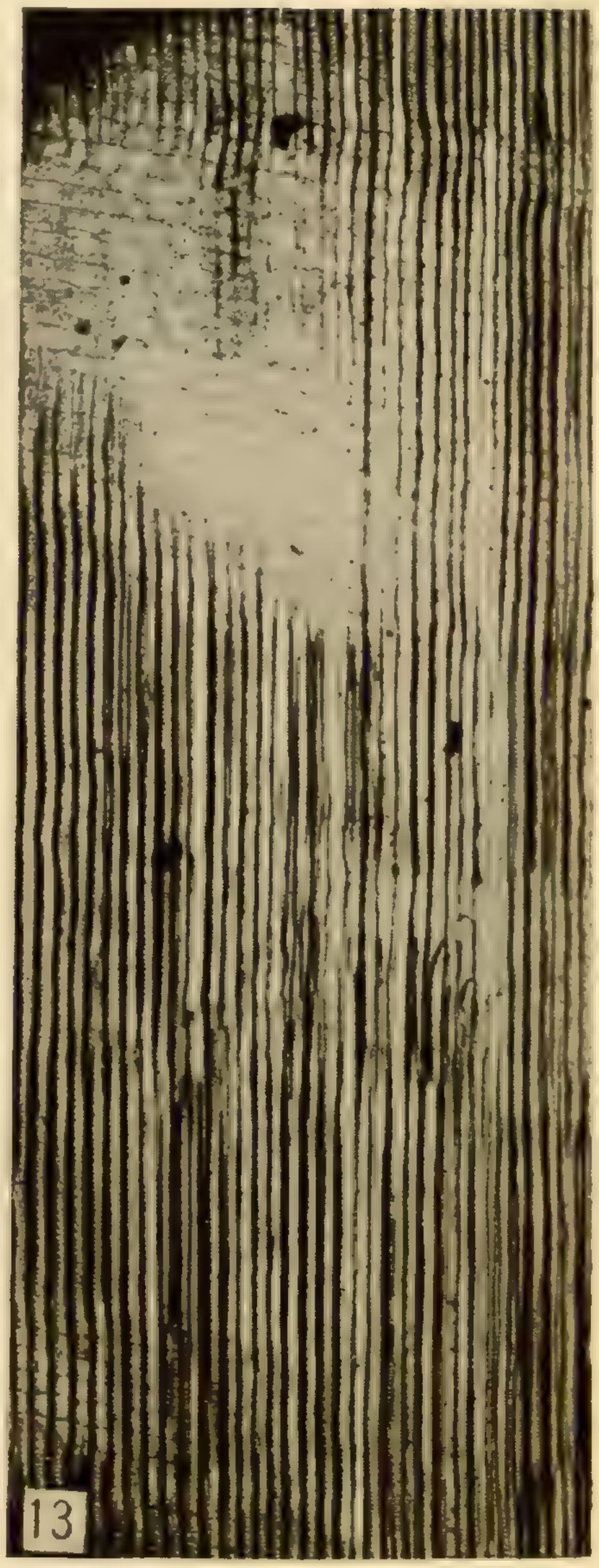
FIGS. 8–11.—*Dioon spinulosum: c*, cone domes; *m*, mucilage ducts; *l*, leaf traces; *p*, phloem; fig. 8, cone dome still separated from the main body of the stele; fig. 9, section at the union of cone dome and main body of stele; fig. 10, slightly more intimate union; fig. 11, longitudinal view of cone dome at point of union with main body of stele; all ×5.

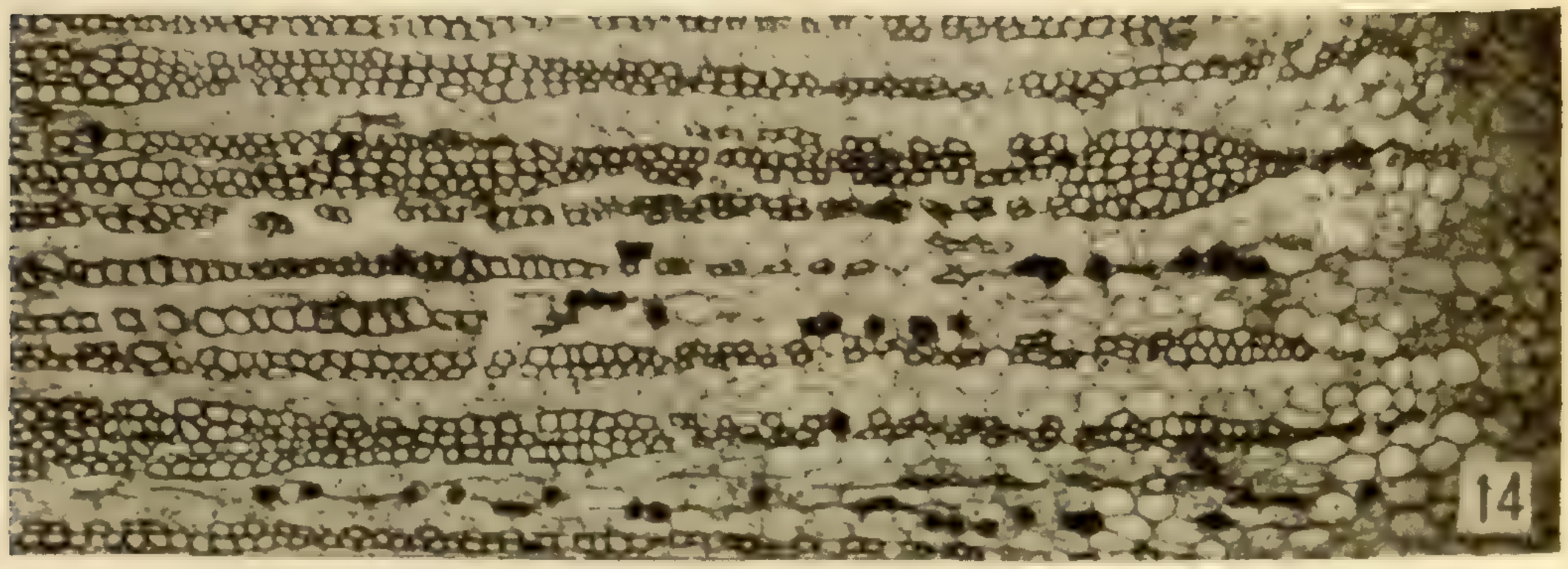
The vascular connections are rather complex. Naturally, each cone dome must, at some point, surround the apex of the preceding cone dome. The general course of the bundles may be seen in fig. 7, which shows three cone domes, the lowest shown in transverse section, the next terminating in the base of an old peduncle, and the upper one passing into a young cone, while at the right of the young cone is the new growing point. It is evident from this figure and the preceding one that the traces of foliage leaves first touch the stele at its periphery, while the bundles of the cone domes are on the inside.

As long as the new dome is separated from the rest of the vascular tissue by a zone of pith, a transverse section looks like a section of a polyxylic stem, except that the smaller zone of vascular tissue is inside (fig. 8); but a little farther down, a transverse section presents a confused array of bundles (figs. 9 and 10). After the bundles of the cone dome and those of the previously formed wood have become arranged into a fairly regular zone, a cambium is established, and the formation of secondary xylem and phloem begins. In uniting with the previously formed wood, the course of the various strands of a bundle is not uniform, some going up, some down, and others entering more or less transversely (fig. 11).

It follows necessarily that every cycad which bears terminal cones must have cone domes in the pith. This would include all the living cycads, with the single exception of the ovulate plant of *Cycas*, in which the sporophylls are borne in a loose crown like the foliage leaves, and the growing point is not transformed into a cone, but remains meristematic. It is possible that in specimens of *Encephalartos*, which produce several cones in a circle, the meristem remains as in *Cycas*. In such a case, no cone dome would be formed; but if at any time such a plant should produce only one cone, or two or more cones in a cluster, a dome would be formed.

In *Macrozamia Fraseri*, WORSDELL (**6**) found numerous bundles in the pith, but claimed that they had no relation to cones. This species usually bears only a single cone, and consequently must have cone domes in the pith. It is possible that WORSDELL'S plant, being a greenhouse specimen, may never have produced a cone, but *Dioon edule*, which elongates very slowly, may show as





FIGS. 12–14.—*Dioon spinulosum:* fig. 12, longitudinal section of mature wood, showing apparently compound nature of the large ray at the upper portion, the bundle at the middle, and mucilage duct lower down; the dark spots are calcium oxalate crystals; fig. 13, longitudinal radial section; fig. 14, transverse section; all ×25.

many as three cone domes in a single transverse section of the trunk, and the arrangement of pith bundles resembles that described for *Macrozamia*. Since the question would be settled by a glance at a longitudinal section of a cone-bearing *Macrozamia* trunk, it is hardly worth while to speculate.

HISTOLOGICAL STRUCTURE

The living trunk of *Dioon spinulosum* cuts rather easily with an ax or machete, but is amazingly difficult to saw. Microtome sections of fresh material are not hard to cut, but transverse and longitudinal sections are likely to break at the large fragile medullary rays. A general view of the histology of the wood is shown in figs. 12–14.

XYLEM.—The xylem, in the older parts of the stem, consists principally of very long tracheids, and is traversed by large and small medullary rays.

Some writers state that there is no protoxylem in the adult cycad trunk, but the statement obviously rests upon a mistaken notion as to the character of protoxylem, such writers assuming that only spiral and annular vessels should be entitled to the name, instead of applying the term to the first xylem differentiated in a bundle, without respect to the character of the markings on the cell walls. The adult stele of *Dioon spinulosum* is endarch, and the protoxylem consists of scalariform tracheids which pass gradually into the pitted tracheids with pointed ends, constituting the principal mass of the xylem. The transition is unmistakable, the scalariform markings, elongated pits, and typical bordered pits sometimes being found in a single tracheid. The bordered pits are multiseriate, two, three, and even five or six rows being found in a radial view of a tracheid, so that in radial sections the wood might be mistaken for that of *Araucaria* (fig. 15). Pits are occasionally found on the tangential walls, but they are not numerous and are irregularly scattered.

Besides the tracheids with pointed ends, the xylem contains elongated cells with transverse walls (figs. 12 and 15–17). These at first are thin-walled and contain starch, but later may or may not become lignified and pitted. They are not uniform in length

or constant in position, although they are most numerous in contact with the medullary rays (fig. 12). That their origin is the same as that of the ordinary pitted tracheid is seen at once in a transverse section of the wood (fig. 17).

Still another form of tracheid is found in the large medullary rays (fig. 18). These tracheids are scalariform, are irregular in outline, and are nearly erect at their upper end, but become nearly

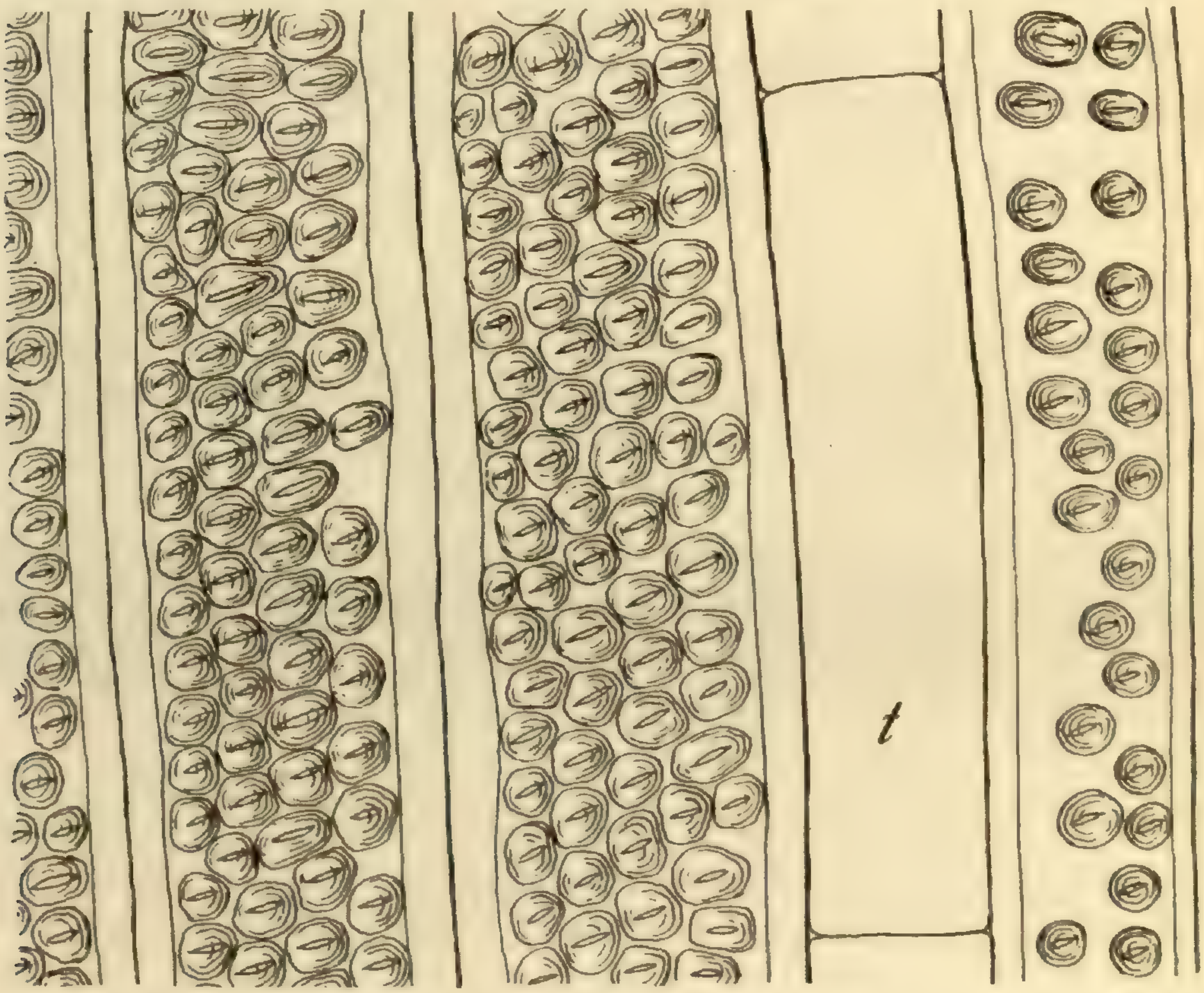
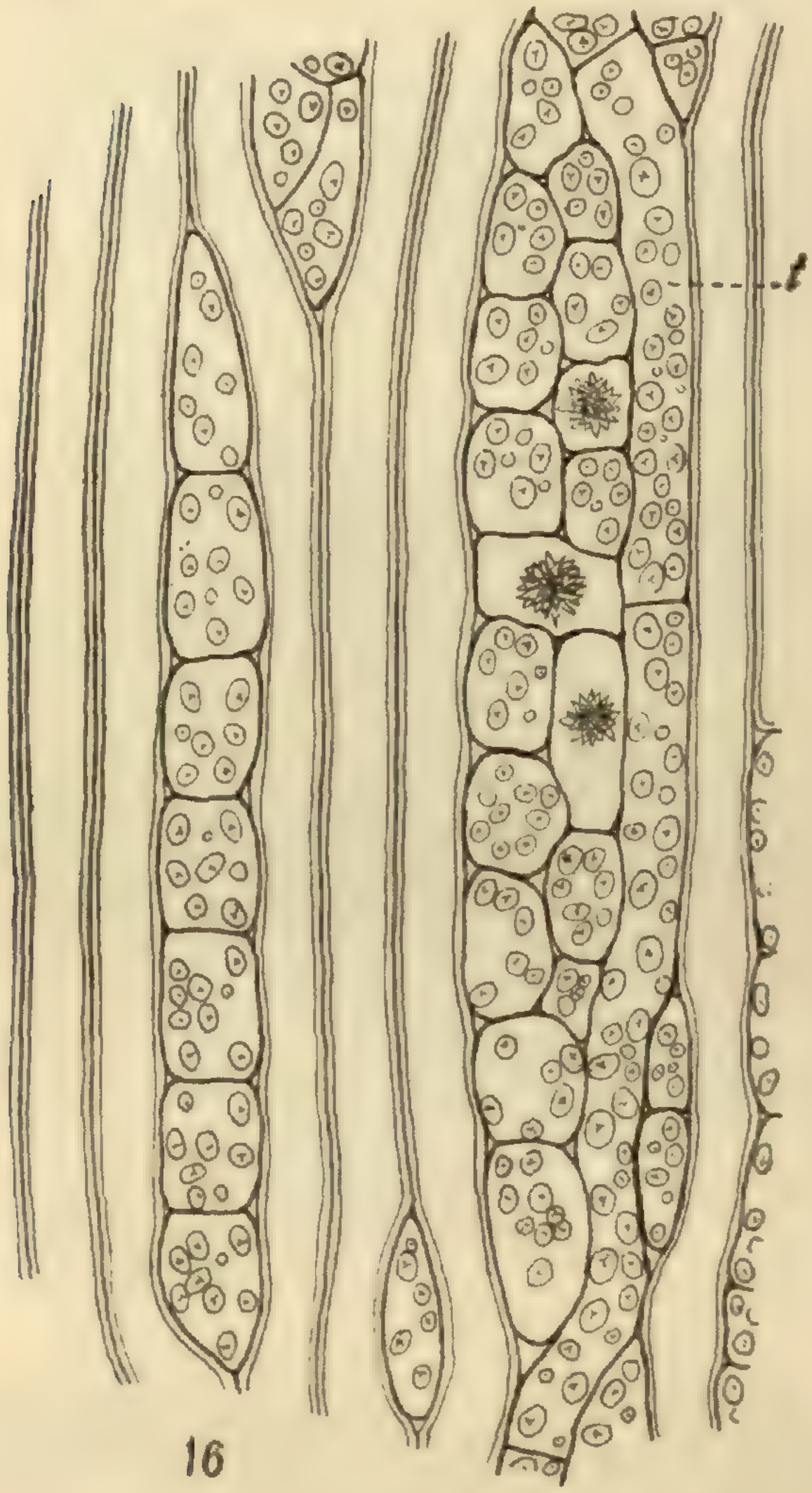


FIG. 15.—*Dioon spinulosum:* longitudinal radial section of mature wood showing multiseriate bordered pits, and also one of the thin-walled cells (*t*) of the xylem; ×390.

horizontal deeper down in the ray, so that a tangential section of the ray shows them in both longitudinal and in transverse section. Every large medullary ray would show these peculiar tracheids at some point or other, and they are particularly numerous near the pith. They connect the leaf trace bundle, which is found in every large ray, with the secondary xylem, a connection hitherto unknown in cycads. Such a secondary connection of the leaf trace is a prominent feature in angiosperms. Professor R. B. THOMSON examined preparations of the large medullary rays, and

I am indebted to him for the suggestion in regard to their connections.

The growth rings, to the naked eye, appear almost as distinct as in dicotyls, but under the microscope they are not so conspicuous (figs. 19 and 20). The latter figure presents one of the most con-



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FIGS. 16, 17.—*Dioon spinulosum:* fig. 16, longitudinal tangential section of mature wood, showing thin-walled cells of the xylem (*t*) containing starch, the xylem tracheids, and the small medullary rays containing starch and calcium oxalate crystals; fig. 17, transverse section showing the phloem with several thick-walled cells, xylem with thick-walled tracheids and several of the thin-walled cells (*t*); *x*, calcium oxalate crystal in medullary ray; both ×125.

spicuous rays which could be found. In *Dioon edule*, the rings appear about the same to the naked eye, but under the microscope are quite distinct, and seem to differ considerably from those of *D. spinulosum*, as might be expected from the description given in

connection with the number of rings. I have not yet found time to give them a careful study. In the plant of *Ceratozamia*, already referred to, the cells of the xylem are quite uniform, there being no trace of growth rings, and a similar condition was found in several stems of *Zamia floridana*.

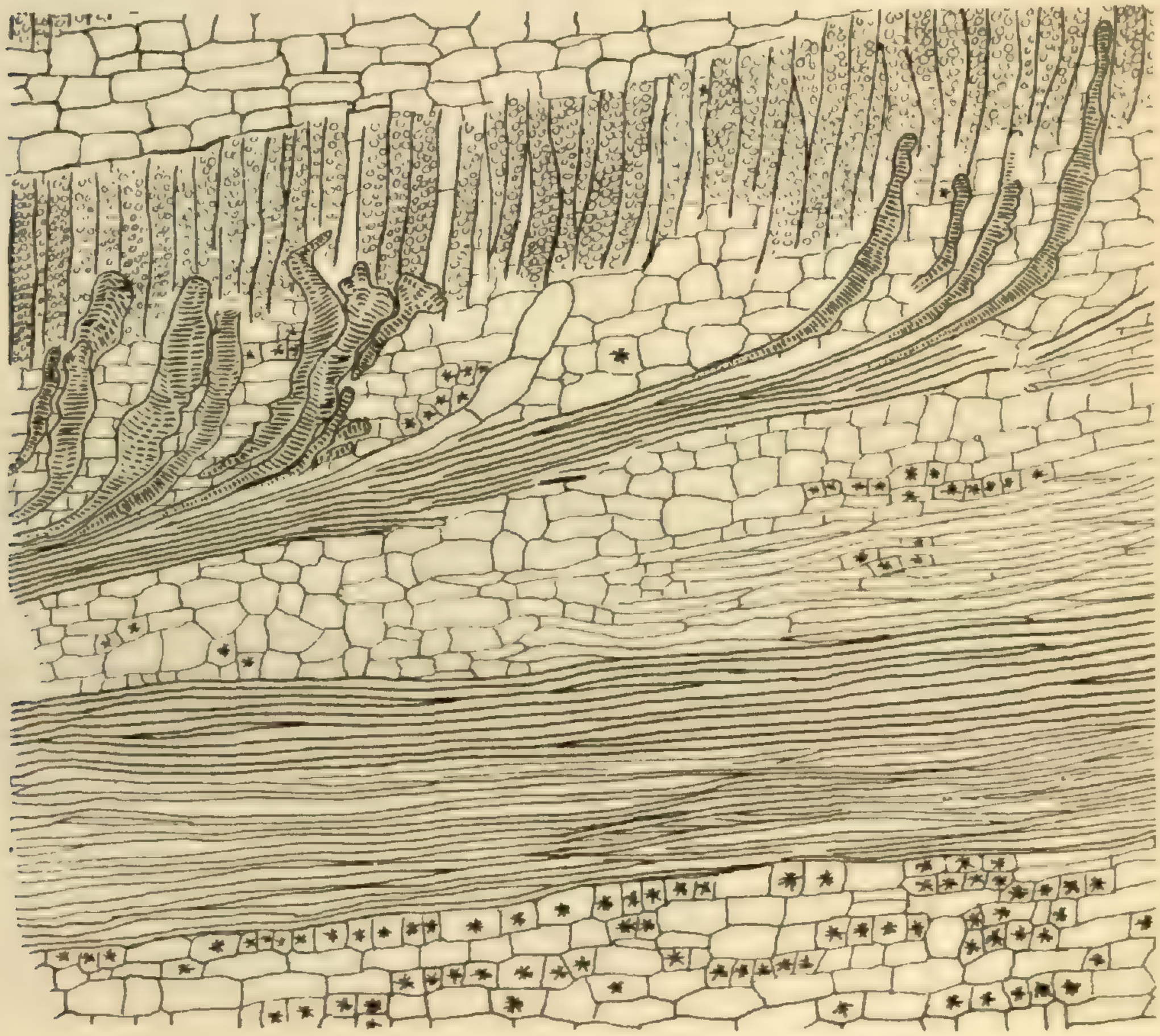

FIG. 18.—*Dioon spinulosum:* portion of large medullary ray, showing the tracheids indicated in tangential section at the tip of the large ray in fig. 12; somewhat above the scalariform tracheids are pitted tracheids of the secondary wood; the lower third of the figure shows part of the leaf trace bundle in the ray; many cells contain calcium oxalate crystals; ×40.

PHLOEM.—The phloem was overlooked by BRONGNIART, doubtless on account of its great extent and the numerous bast fibers which makes it resemble the wood. A small portion of the xylem, the cambium, and a small portion of the phloem of *Dioon spinulosum* are shown in fig. 17. The extent of the phloem is indicated in the photomicrographs (figs. 3, 4, and 8–10). In longitudinal section, especially in tangential section, the resemblance to the wood is

even more striking, the medullary rays being just the same, and the bast fibers having about the same arrangement as the long tracheids of the xylem. This structure makes the phloem nearly as rigid as the wood.

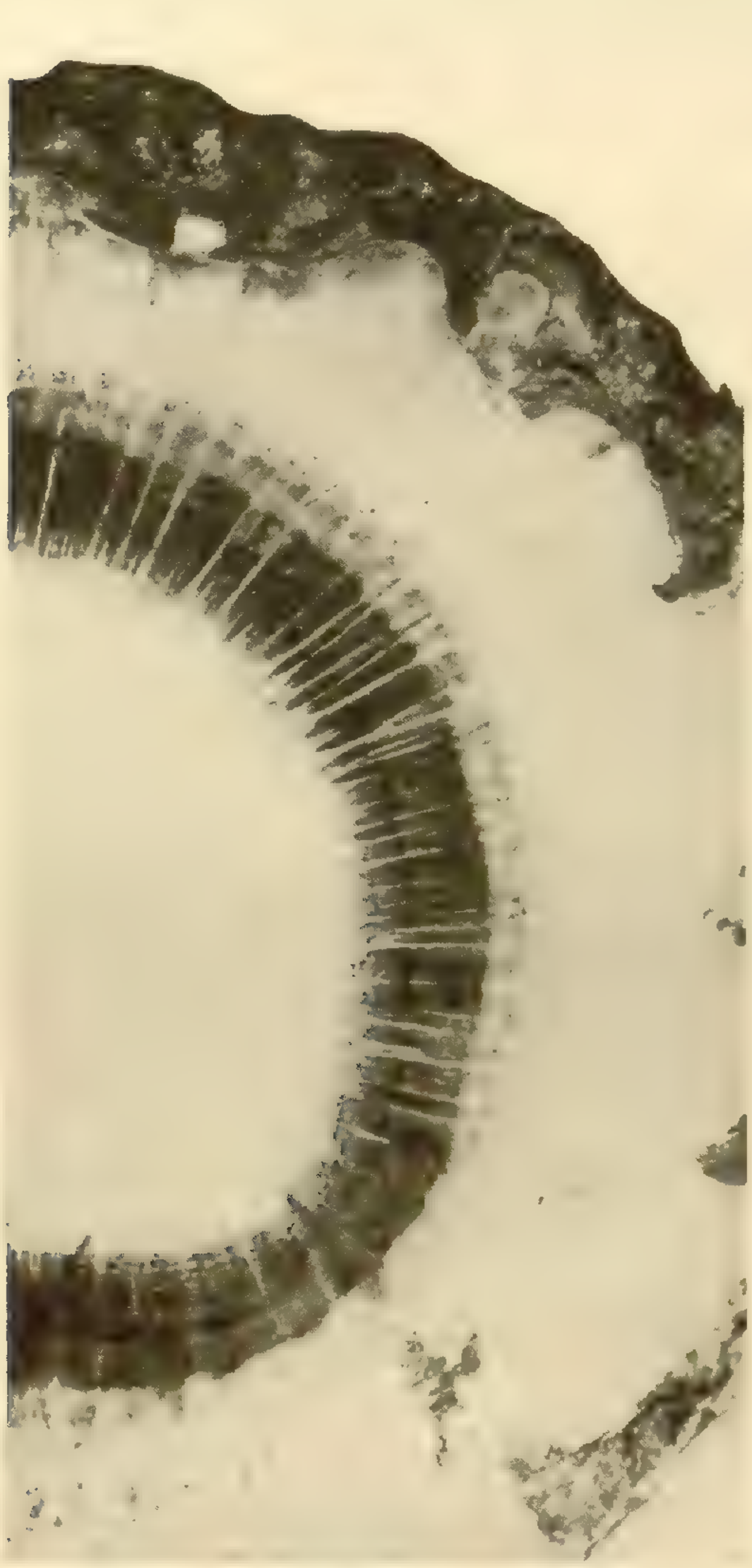

FIG. 19

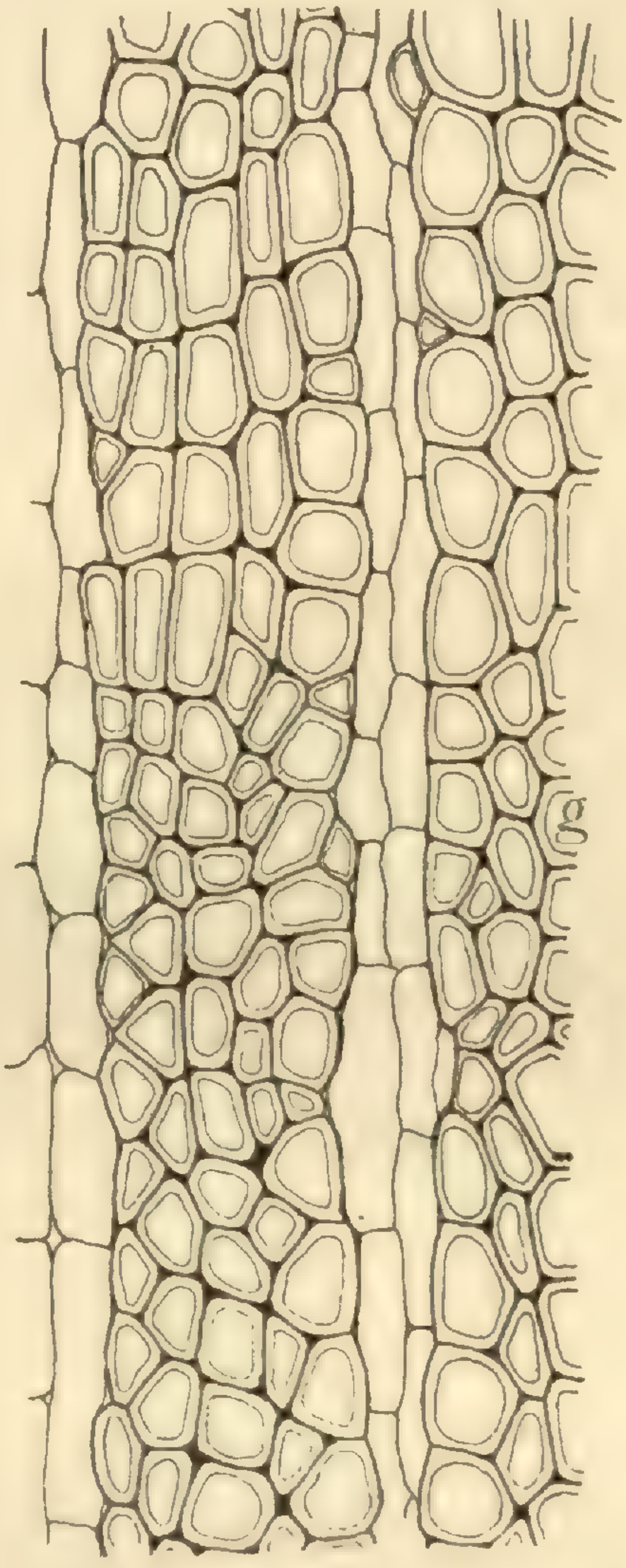

FIG. 20

FIGS. 19, 20.—*Dioon spinulosum:* fig. 19, photograph showing growth rings, ×¾; fig. 20, a single growth ring (*g*); ×125.

RAYS.—In a transverse section the large medullary rays are as conspicuous as those of *Quercus*, and the small rays, while not nearly so conspicuous, are readily visible to the naked eye (fig. 3).

The small rays vary greatly in longitudinal extent, some showing only a single cell in tangential section, while others may show more than 50, and may reach a width of 3 or 4 cells. The great

majority of the small rays are less than 20 cells in longitudinal extent, and are one or two cells wide, often two cells wide in the middle and one cell wide at both ends (fig. 12). Radially, the rays extend from the pith to the cortex, few if any new rays being formed as the trunk grows. Most of the cells contain large starch grains, but some have crystals of calcium oxalate, which is also abundant in the phloem, cortex, and pith.

The large rays also extend from the pith to the cortex. Longitudinally, they measure 4 to 8 mm., and from a width of about 1 mm. in the middle they taper to a single cell above and below. In each large ray is a leaf trace, with its phloem more or less disorganized. The xylem of this bundle is usually uppermost, but the orientation is various until the bundle reaches the cortex, where it becomes a part of the characteristic girdle. From both the pointed ends, tracheids extend into the ray, often making nearly half of the ray look like a group of small rays (fig. 12). Most of these tracheids which extend into the rays are scalariform, but some are slightly pitted, and some are the cells of the wood with transverse walls already described. Every large ray has at least one mucilage duct, and surrounding it at a distance of a few cells, the calcium oxalate crystals are particularly abundant.

While the large ray, especially in tangential section, resembles the broad ray of *Quercus*, as described by EAMES (9), its mode of formation is different, the broad ray of *Quercus* originating by the fusion of small rays, while in *Dioon* the broad ray owes its origin to the leaf trace which it contains. The tissues simply grow around the leaf trace, and the compound appearance of the ray, shown at the upper end of the photomicrograph (fig. 12), is a secondary, not a primary feature.

COMPARATIVE HISTOLOGY.—The trunks of *Dioon spinulosum*, *D. edule*, *Ceratozamia mexicana*, and *Zamia floridana* have some histological characters in common, and it is probable that all the Cycadales have enough histological peculiarities to identify the order by the structure of the trunk. The four species mentioned above are easily distinguished from each other by such histological characters, but it is very doubtful whether nearly related species of a large genus like *Zamia* could be so distinguished from each

other. The distinction would doubtless be mu more difficult in young trunks than in old ones.

The structure of the trunk of *Dioon spinulosum* is remarkably like that of the Bennettitales. The growth rings resemble those of *Cycadeoidea Jenneyana*, as described by WIELAND; the phloem, with its numerous thick-walled fibers in transverse section, is very similar to that of *Cycadeoidea Wielandi;* and the xylem, as it abuts upon the pith, also resembles that of *Cycadeoidea*. But there are also contrasting features; the broad medullary rays are not figured in the Bennettitales, and in the xylem cells with transverse walls seem to be lacking.

Summary

1. The paper deals with field material of adult stems of *Dioon spinulosum*, *D. edule*, *Ceratozamia mexicana*, and *Zamia floridana*, particular attention being given to *Dioon spinulosum*.

2. In *Dioon spinulosum* the xylem zone in a plant 6 meters in height reaches a width of 10 cm., far exceeding the extent of any xylem zone previously described for any cycad.

3. *Dioon spinulosum* and *D. edule* have growth rings, which in *D. spinulosum* correspond to the periods of activity which result in the formation of crowns or cones, but which in *D. edule* do not correspond to such periods. No growth rings were found in *Ceratozamia mexicana* or *Zamia floridana*.

4. Cone domes in the pith were studied in the four species.

5. The histological character of the adult stem was studied in *Dioon spinulosum*. The protoxylem consists of scalariform tracheids, from which there is a gradual transition to the tracheids with multiseriate bordered pits, constituting the principal part of the wood. There are also cells with the same origin as the pitted tracheids, but with transverse walls which may remain thin-walled and contain starch or may become lignified. Besides the leaf trace bundles, scalariform tracheids are found in the large medullary rays.

6. Both in the general appearance of the transverse section and in histological characters the adult trunk of *Dioon spinulosum* resembles that of *Cycadeoidea*.

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A BOTANICAL SURVEY OF THE HURON RIVER VALLEY

VIII. EDAPHIC CONDITIONS IN PEAT BOGS OF SOUTHERN MICHIGAN

GEORGE PLUMER BURNS

(WITH EIGHT FIGURES)

In a paper read before the Society for Plant Morphology and Physiology at the Philadelphia meeting (1904), the author called attention to the fact that the plants in peat-forming lakes near Ann Arbor, Michigan, are by no means all xerophytic. With xerophytes are found many plants whose structure is either mesophytic or hydrophytic, and the conclusion was drawn that in the vicinity under consideration one should no longer refer to a peat bog, as such, as a xerophytic habitat (**2**).

TRANSEAU (**17**), in a very interesting paper dealing with the distribution of bog and swamp plants, stated that the two were found growing together in the bogs of southern Michigan, and accounted for the present mixture of the two kinds chiefly on historical and climatic grounds.

PENNINGTON (**13**) concludes that the bogs in southern Michigan are heterogeneous habitats and demand detailed study.

LIVINGSTON (**12**), DACHNOWSKI (**7, 8**), and TRANSEAU (**18**) in experimenting with bog water have found that it is not the same in all zones. The samples of water taken for experimental purposes were generally from under *Larix*, *Drosera*, *Sarracenia*, *Andromeda*, *Cassandra*, *Vaccinium*, *Eriophorum*, etc., that is, from zones with marked xerophytic plants.

The distribution and position of zones of plants in the bogs of southern Michigan have been given by DAVIS (**9**), TRANSEAU (**18**), the author (**3, 4**), and others. On the side of greatest depth the following zones are found:

I. *Zone of submerged plants*.—Plants in this zone usually do not go to great depths. In many lakes no vegetation is found at a depth of 12 feet (3.66 m.). The chief plants are *Chara*, *Cera-*

tophyllum demersum, *Naias flexilis*, *Potamogeton lucens*, *P. natans*, *P. zosteraefolius*.

II. *Zone of water lilies*.—This zone is confined to shallow water seldom over 5 feet (1.5 m.) in depth. The characteristic plants are *Castalia odorata*, *Nymphaea advena*, *Brasenia Schreberi*.

III. *Zone of floating sedges*.—The mat formed by these sedges is very firm and usually about 18 inches (45.8 cm.) in thickness. The chief mat-forming plants are *Carex filiformis* and *C. oligosperma*. Associated with these, some playing an important part in mat-formation, are *Menyanthes trifoliata*, *Dulichium arundinaceum*, *Eriophorum viridi-carinatum*, *Drosera rotundifolia*, *Aspidium Thelypteris*, *Onoclea sensibilis*, *Equisetum limosum*, *Eupatorium purpureum*, *E. perfoliatum*, *Mentha arvensis* var. *glabrata*, *Scutellaria galericulata*, *Utricularia* sp., *Calopogon pulchellus*, *Campanula aparinoides*, *Arethusa bulbosa*, *Galium trifidum*, *Aster junceus*, *Potentilla palustris*, *Solidago serotina* var. *gigantea*, *Lysimachia terrestris*, etc.

IV. *Zone of bog shrubs*.—The characteristic plants of this zone are *Chamaedaphne calyculata*, *Andromeda polifolia*, *Betula pumila*, *Nemopanthes mucronata*, *Sarracenia purpurea*, *Vaccinium Oxycoccus*, *V. macrocarpon*.

V. *Zone of tamaracks*.—The principal plants are *Larix laricina*, *Cornus stolonifera*, *Osmunda regalis*, *O. cinnamomea*, *Rhus Vernix*, *Aster junceus*. In areas where the tamarack is thick there is no undergrowth.

VI. *Zone of poplars and maples*.—This zone is often of great width for reasons pointed out in a previous paper (**4**), and has the greatest variety of species of any zone. Some of the plants found are *Acer rubrum*, *A. saccharinum*, *Populus tremuloides*, *P. grandidentata*, *Prunus serotina*, *Quercus rubra*, *Q. bicolor*, *Sambucus canadensis*, *S. racemosa*, *Salix discolor*, *S. rostrata*, *Spiraea salicifolia*, *Cornus stolonifera*, *Ilex verticillata*, *Cephalanthus occidentalis*, *Rosa carolina*, *Epilobium adenocaulon*, *Verbena hastata*, *Solanum Dulcamara*, *Polygonum sagittatum*, *P. hydropiperoides*, *Geum rivale*, *Rumex britannica*, *Impatiens biflora*, *Viola blonda*, *Solidago canadensis*, *S. graminifolia*, etc.

VII. *Zone of marginal willows*.—*Salix nigra*, *S. lucida*, *S. dis-*

color, *Cornus stolonifera*, *Ilex verticillata*, *Rubus idaeus* var. *aculeatissimus*, *R. hispidus*, *R. villosus*, *Rosa carolina*, *Vitis vulpina*, *Alisma Plantago-aquatica*, *Acalypha virginica*, *Agrostis alba*, *Bidens cernua*, *Cicuta bulbifera*, *Carex vulpinoidea*, *C. scoparia*, *Eleocharis tenuis*, *Eupatorium perfoliatum*, *Geum strictum*, *Glyceria nervata*, *Juncus effusus*, *Lycopus americanus*, *L. virginicus*, *Lactuca canadensis*, *Ludvigia palustris*, *Pilea pumila*, *Polygonum Hydropiper*, *P. sagittatum*, *Penthorum sedoides*, *Ranunculus pennsylvanicus*, *R. scleratus*, *R. delphinifolius*, etc. (fig. 1).

FIG. 1.—First Sister Lake near Ann Arbor, Mich.; the photograph shows the zonal arrangement of plants at the southwest corner; five zones can be distinguished as follows: water lily, bog sedge, bog shrub, tamarack, maple-poplar; the adjacent uplands are covered with oak-hickory woods; photograph by STEELE.

A study of the partial lists given above shows that they are not all xerophytes. There are at most only three zones which have bog flora as the characteristic plants. These are the floating sedge, the bog shrub, and the tamarack zones. In the first of these only those plants rooting deep in the mat can be called bog xerophytes; those rooting in the surface layers are hydrophytes. The other zones are occupied by hydrophytes or mesophytes.

The flora of the postglacial lakes studied in southern Michigan may be classified thus:

Vegetation in postglacial lakes	Hydrophytes	Submerged plants
		Water lilies
	Xerophytes	Floating sedges
		Bog shrubs
		Tamaracks
	Hydrophytes or mesophytes	Poplar-maples
	Hydrophytes	Marginal willows

An investigation has been carried on for several years by the author and some of his advanced students to determine as far as possible the edaphic conditions in the different areas outlined above. A short report has been given (**5**) and a more detailed account of some of the results is given in this paper.[1]

Temperature

The aerial parts of the bog plants are subjected to great extremes in temperature. Situated, as they are in the area under discussion, in low basins with often very steep sides, the air from the adjacent uplands drains into them, producing a temperature several degrees lower than that on the surrounding uplands during the night and early morning. During the day, however, very high temperatures have been recorded. Such temperatures have also been recorded by GANONG (**10, 11**) in New Brunswick.

Unless otherwise stated in the text, all temperature readings given in this paper, both for soil and air, were taken with Richard Frères, Paris, thermographs belonging to the University of Michigan. These instruments are shown in fig. 2 in the shelter in which they were kept in the field. The one on the left records the air, the other the soil temperatures. It was found, unfortunately, that the soil thermometer was unreliable when the tempera-

[1] Bog conditions in southern Michigan, which lies toward the southern limit of their distribution in this country, seem to be quite different from bog conditions farther north described by GANONG (**11**). This point was emphasized also by TRANSEAU (**17, 18**). See also BASTIN and DAVIS (**1**).

ture of the air fell near the freezing point, and hence the early spring and late fall data were untrustworthy. In any temperature of the air ranging above 7° C., the records were found to be reliable.

The temperature of the air at First Sister Lake, in the floating sedge zone, compared with that on high ground in Ann Arbor at 7 A.M. is given below.

FIG. 2.—Thermographs in the bog shrub zone at First Sister Lake; the one on the left is recording air, the other soil temperature; photograph by STEELE.

TABLE I

DIFFERENCES IN TEMPERATURE IN BOG AND UPLAND; BOTH RECORDS WERE MADE WITH THERMOGRAPHS

WEEK	HIGHEST		LOWEST	
	Bog	Upland	Bog	Upland
April 26–May 3	5° C.	14°.7 C.	−1° C.	2°.4 C.
May 3–May 10	7	10.1	4	0
May 10–May 17	11	18	−1	0
May 17–May 24	10	14.2	−2	3.6

Table I shows that in the morning the temperature of the air in the bog is several degrees lower than that of the upland. The only exception in a much larger collection of data than published

here was seen in the lowest point reached during the second week when the upland went to 0, while the bog remained 4° warmer.

The records of the thermographs show wide variations in air temperatures. In 1907, during the week April 26–May 3, it ran from 21°.5 C. to −4°.5 C.; in 12 hours it rose from −4°.5 C. to 16° C.; May 11, from 6 A.M. to 8 A.M., the air was −4° C.; May 13 at 1 P.M. it reached 28° C.; May 16 at 3 A.M. it was only 1°.5 C. Low temperatures were recorded during the summer. On June 28 the air got as low as 4° C. July (1907) was the hottest month, judged from the lowest temperatures reached, the lowest for the month being 7° C. at 6:15 A.M. the 27th. In August the low records were: the 1st, 9° C.; 3d, 6° C.; 4th, 6° C.; 13th, 7° C.; 22d, 3°.5 C.; 25th, 5° C. August 6, 1904, a maximum-minimum thermometer was hung in the top of an 8-foot tamarack in the sedge zone at Dead Lake. It showed a maximum of 37°.8 C. and a minimum of 5°.5 C.

These figures show that the temperature of the air is comparatively low during the entire summer during the night. The coldest time came at 1 A.M. or about 7 A.M. On the other hand, day temperatures may run very high. The hottest time of the day was about 1 P.M.; it seldom came as late as 2 P.M. Fig. 3 reproduces the air record for the week July 2–9, 1906, taken in the floating sedge zone at First Sister Lake.

The temperature of the soil, on the other hand, shows very slow variations during the season. There is great difference in soil temperatures at different depths, and they warm up very slowly, except for the shallow surface layer; they never get very cold. When making contour maps of the bottom of these lakes (**3, 4**) in winter, it was soon learned that although the ice might be 10 inches (25.3 cm.) thick over open areas, a good thrust of the drill would usually send it through the thin ice near and beneath the tamaracks. Even in most severe weather it was necessary to wear rubber boots, as the thin ice continually broke under one's weight. What ice is formed, however, lasts long into the spring.

In taking soil temperatures, a square piece was sawed out of the peat and carefully removed. The long bulb of the thermo-

graph was then inserted in the side of the opening parallel to the surface for about 18 inches (45.8 cm.), and the piece of peat was replaced. The surface arrangement was left as nearly normal as possible. Some of the records were made at Dead Lake, but most of them were made at First Sister Lake.

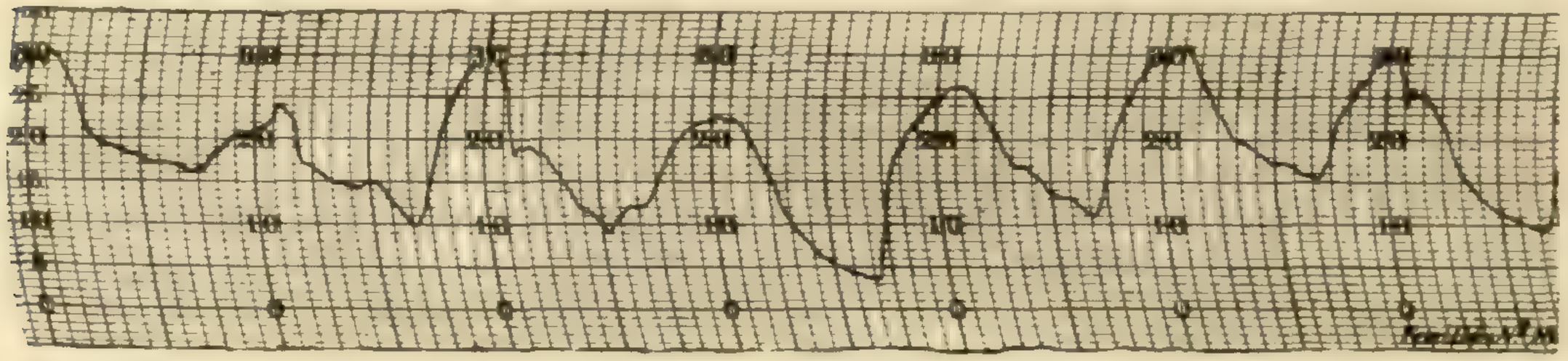

FIG. 3.—Temperature record of the air for the week July 2–9, 1906, taken in the sedge zone at First Sister Lake; the highest was 31° C., the lowest 3°.5 C.; this occurred about 5 A.M., July 6.

Fig. 4 shows a partial record of the results which were obtained at the latter lake at different depths in the tamarack zone. *A* is taken from the figures of TRANSEAU (**18,** p. 421) and gives the readings at a depth of 1 inch (25 mm.). At this depth the rise in temperature is quite rapid and resembles that of the adjacent uplands. At the time the leaves began to appear, May 27, it had reached 17° C. Line *B* gives the record for a depth of 4 inches

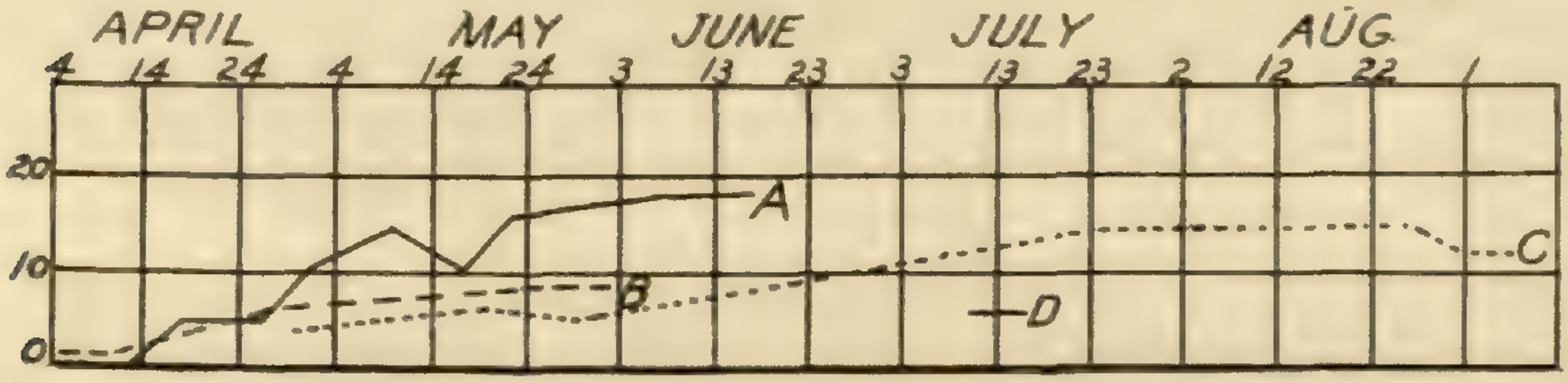

FIG. 4.—Diagram showing variation in temperature at different depths and at different seasons in the tamarack zone; *A*, 25 mm.; *B*, 10.2 cm.; *C*, 20.4 cm.; *D*, 45.8 cm. below the surface.

(10.2 cm.) to June 1. The temperature at this point does not rise so rapidly as that just given, and on May 25 had reached 9° C. The dotted line *C* gives the temperature at 8 inches (20.4 cm.). This record shows that during the spring, when leaves are unfolding, the soil temperature at this depth remains comparatively low; not until July 22 did it reach 14° C. This was held for about a month (July 22–August 24), when it gradually began

to lower. The readings given in line *D* were taken 18 inches (45.8 cm.) below the surface, and were continued for only a short time; the temperature was surprisingly low.

The next figure (fig. 5) was furnished by Mr. HAROLD STEELE, and gives the results of short readings in several zones. These readings were made in 1904 at the same lake. The soil readings

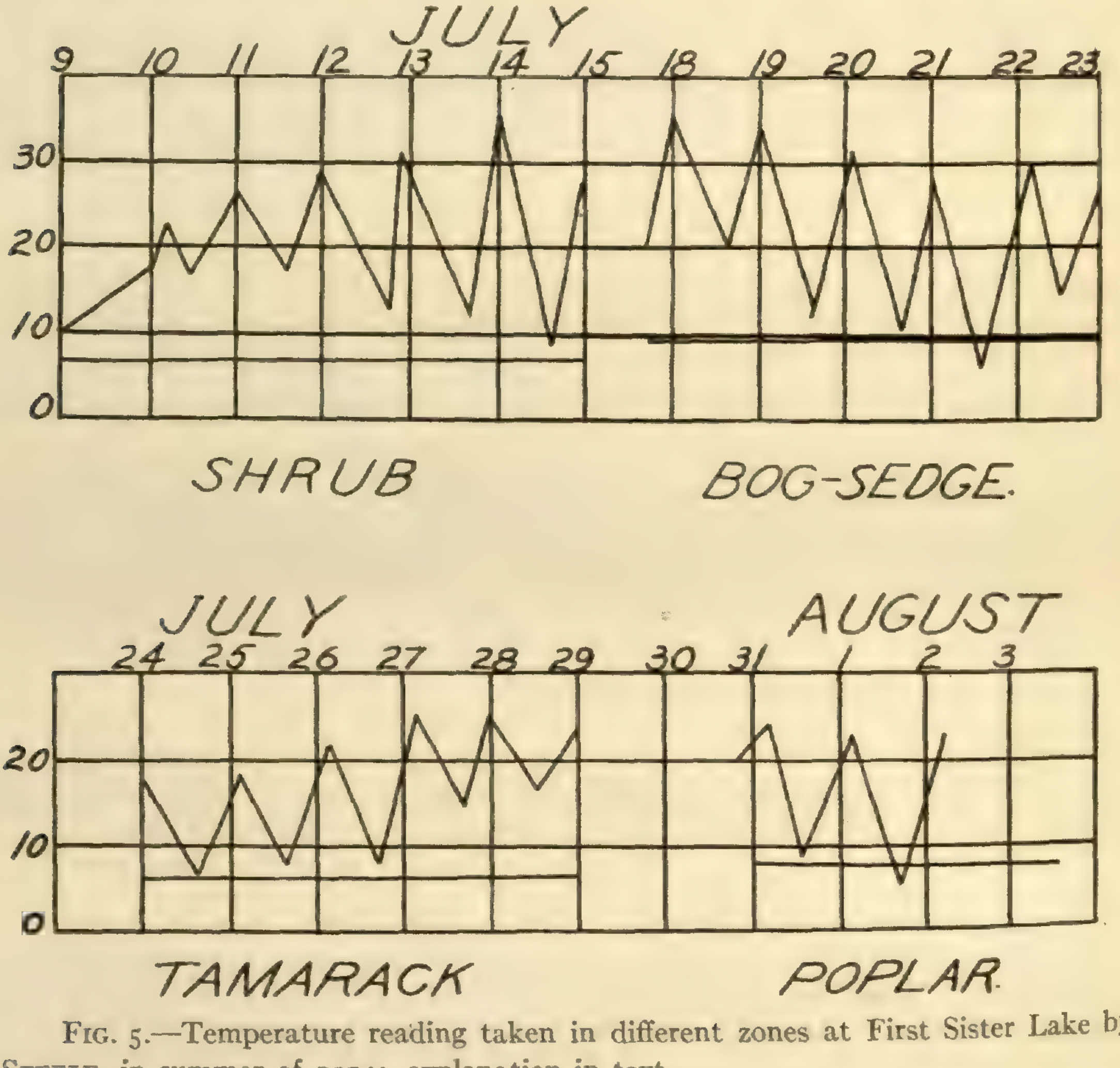

FIG. 5.—Temperature reading taken in different zones at First Sister Lake by STEELE, in summer of 1904; explanation in text.

are taken 18 inches (45.8 cm.) below the surface. This shows that the soil under the tamaracks is the coldest. The same is reported by TRANSEAU (**18**). As the writer had only one set of thermographs at his command, the readings could not be made simultaneously, but the data gathered seem to show that this made little difference in this case, as the temperatures were stationary. The soil temperatures were: tamarack, 6° C.; bog shrub, 7°.5 C.; poplar, 7°.5 C.; and bog shrub, 10° C. These

temperatures for the last two were lower than the author obtained for these zones. As has been pointed out, there is great variation in the poplar zone, and one should have a better knowledge of the exact location before attempting to explain this difference. The temperature under the bog sedge also varies with the width of the floating bog and the proximity to the zone of bog shrubs. That is, the temperature remains more constant when one gets away from the open water.

Average records made by a class with ordinary thermometers for six weeks in the summer of 1906, 3 inches (7.6 cm.) below the surface, were as follows: open water, 18° C.; bog sedge, 17° C.; tamarack, 15° C.; maple-poplar, 17° C.; marginal willows, 18° C.; outer edge of marginal zone with no shade at 1:15 P.M., 22° C.

These readings show a wide divergence of soil temperatures in the zones under consideration, and also at different depths in the same zone. This calls for a study of the depth of the root systems. For example, the high temperature of the soil at 25 mm. represents the condition for germination of the many seeds of "drained swamp" plants which yearly lodge in the bog. This taken with the weak light and humid air, which will be considered later, makes an excellent place for germination of these seeds. On the other hand, the study of the root system shows that temperatures found at a depth of 45.8 cm. in the bog sedge and tamarack zones, especially, could not have a direct influence on the plants growing above, as they did not root in that layer but only in the surface layers. This is true even of the largest trees. Added to this fact is the additional consideration that peat is a very poor conductor of heat. The soil readings in these zones which are of the greatest importance are those taken near the surface in a study of reproduction, and those at moderate depths in the study of the present flora.

These data become ecologically important in the light of the work of TRANSEAU (**18,** p. 22), who has shown by experiment that a temperature of 10°.8 C. causes a diminution in the development of both roots and leaves. Although the trees began to open their buds the last of May, it was not until July that the temperature about the roots of the tamaracks reached a higher temperature.

This was after the most active vegetative period. Conditions in the bog shrub zone closely resemble those just described. In bog sedge the records show less regularity and resemble more closely swamp conditions, especially, as has been said before, in bogs where this zone is narrow.

In the two outer zones, the temperatures recorded resemble more closely the upland and drained swamp conditions. Here they ranged about 18° C., in July reaching this mark early in the summer. They would have a less detrimental effect upon the root systems of the plants in these zones.

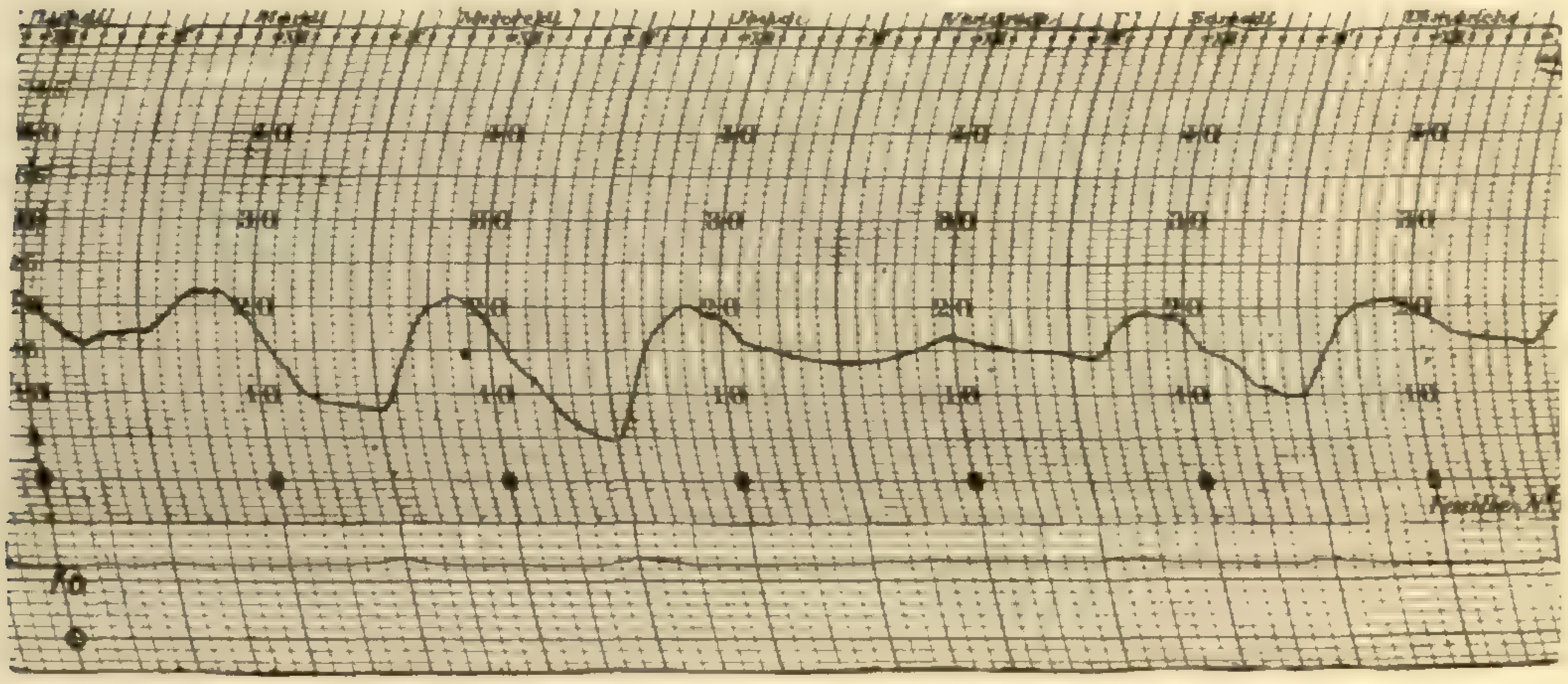

FIG. 6.—Record of soil and air temperatures made at First Sister Lake, Ann Arbor, Mich., August 23–30, 1907; the instruments were in the bog sedge zone; the bulb of the soil thermograph was 20.4 cm. below the surface; the upper line shows record of the air, the lower the soil thermograph.

Fig. 5 also shows the range of air temperatures for the periods given above. The results are similar to those already given by the author.

The record of the soil and air thermographs for one week, August 23 to August 30, is reproduced in fig. 6. This is only one of numerous records which were taken, and shows the very slight variations in the temperature of the soil and the great variations in the temperature of the air. The greatest variation in soil was about 1° C.; that of the air was 17° C. In fig. 3, the variation in air temperature was 25°.5 C.

Water table

The variations in the position of the water table from year to year and from month to month play a very important part in the succession of plant societies in these bogs. In 1908 the level of the water in all bogs of southern Michigan was high. In 1901–1904, when the maps of Dead Lake were made (3), there was an island near the center, and it was customary to row out there and leave the supplies when working at the lake. That island in 1908 was submerged, and one could row over it in 18 inches (45.8 cm.) of water. The flora of upland forms had disappeared with the exception of some stunted willows, and in its place were a few potamogetons, chiefly *P. heterophyllus*. At Whitmore Lake, north of Ann Arbor, the same rise in water has occurred, and what was a peninsula in 1904 is now an island. The same fact is recorded by DAVIS (**9,** p. 162).

During a series of wet years the change in water level affects the vegetation in all zones except perhaps on the lakeward side of the floating sedge, which rises and falls with every change of level. Along shallow shores the factor is sufficient to control the character of the vegetation, as has been pointed out in the case of the island at Dead Lake. Its influence is also profound in those zones where the peat is solid. It may rise above the surface to a depth of several inches. With this rise there is also found an increase in the humidity of the air. During such periods *Sphagnum* sp. spreads rapidly toward the shore and may assume quite an important position in all zones except perhaps the marginal. An interesting example of the behavior of this moss during wet and dry periods is found at Mud Lake. Here a section was made which showed alternating layers of *Sphagnum* and *Polytrichum* corresponding to the wet and dry periods of previous years. As many as four layers were easily distinguished at Mud Lake.

In one case measured the shrubs stood in water which was 18 inches (45.8 cm.) deep one summer, and in water of various depths less than that for a period of at least three years. These plants then must be able to endure submergence for a long period, as has been pointed out by DAVIS.

During wet periods bog plants show a tendency to move shoreward. This is due to local conditions rather than to historic factors. Such movement is only temporary.

In the summer of 1909 the island in the center of Dead Lake had begun to reappear. During the late summer the ground appeared in the higher parts, showing that the water level was getting lower. In less than ten years the island disappeared and in part reappeared, which indicates that these wet and dry periods may be of short duration. This is contrary to the belief, often expressed, that in southern Michigan they last about thirty years each.

The effect of the dry periods upon vegetation is also very marked. The relation of such periods to plant succession has been emphasized by DAVIS, who believes that they offer an explanation of the xerophytic structures of bog plants (**9**, p. 160). During such periods the surface layers of the peat become exceedingly dry; this may extend to a depth of several feet. Fires which reduce the surface several feet are of common occurrence. The effect of fires upon plant succession has been given by PENNINGTON (**13**).

During this time there is very little water available in these surface layers for plants, and, as it will be shown later that the movement of water in peat is slow, it can easily be seen that the habitat is very dry, even omitting the usual factors of humus acid, low temperature, bog toxins, etc. The following table is given by DAVIS taken from WARRINGTON (**19**).

TABLE II

PARTS OF WATER PER 100 PARTS OF DRY SOIL

Type of soil	When plants wilted	Absorbed from moist air
Coarse sandy	1.5	1.15
Sandy garden	4.6	3.00
Fine humus sand	6.2	3.98
Sandy loam	7.8	5.74
Calcareous	9.8	5.20
Peat	49.7	42.30

DAVIS says: "If these results are correctly reported, it appears that peat may appear very wet and yet contain no water for plants growing in it, so that

those plants which habitually grow at levels of peat bogs, where the surface strata can dry out, must have xerophytic adaptations if the climate is such that drying out of these levels may occur."

In addition to the variation in water level due to wet and dry periods, there is the variation from month to month during each year. This difference is shown in fig. 7, which gives the results obtained April 20–August 3, 1905, in the zones at First Sister Lake. The data were gathered for the most part by STEELE. Holes were

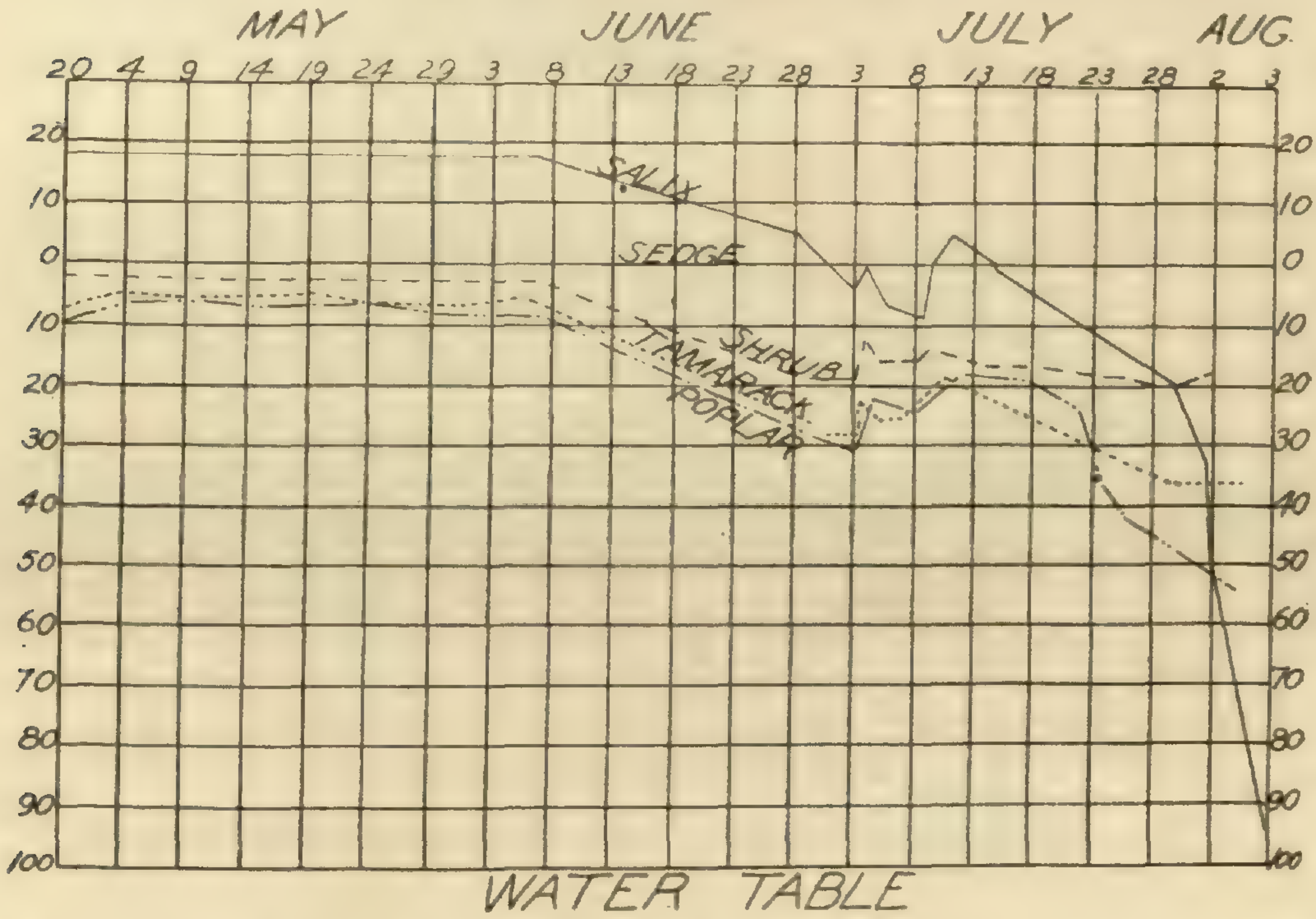

FIG. 7.—The results of measurements taken to determine the variations in water table in the different zones at First Sister Lake; variations are given in cm.

dug in the peat of the different zones to a considerable depth, and a stick placed in a horizontal position at the top. From this stick measurements were taken daily to the top of the water standing in the holes. These were plotted and the result shows in the figure just given.

The bog sedge zone shows practically no variation, although there would have been some, especially on the landward side, had the measurements been started very early in the spring. This however would be too early to affect the vegetation. The open water shows some variation in the summer, but the bog

sedge rises and falls with it, and there is little variation during the growing season.

The other zones show a gradual lowering of the water table, beginning quite rapidly June 8 and continuing until July 3. At this time a heavy rain fell, raising the water level sharply in all zones. After this there was a rapid lowering of its position in all zones until the close of measurements, except in the bog shrub; this showed a slight rise.

The greatest variation, as has been said, was in the marginal zone. On April 20 the water was 7.2 inches (18 cm.) above the surface of the peat. This gradually lowered until the water table was 38.4 inches (96 cm.) below the surface. A variation of 45.6 inches (113 cm.) was recorded.[2] In the maple-poplar zone the variation was 18.4 inches (46 cm.); in the tamarack zone, 12.4 inches (31 cm.); in the bog shrub zone, 6.8 inches (17 cm.). These figures show that the loose peat acts as a dam, holding the open water in the lake from flowing back to the outer zones. The same fact was reported by a former student (**14**) at the small bog near Carpenter's Corner. Here a central area was found with the characteristic bog flora of this region, while the greater part of the original lake was occupied by a mixed flora, with red maple and poplar as the dominant trees. This seemed to be an example of the "lagging behind of a xerophytic group of plants in a hydrophytic habitat," but borings showed that the water table was only 1.4 inches (6 cm.) from the surface. The temperature of the soil and character of the peat were the same as generally found under such plants. A few rods to the east, under the maples, the water table was several feet below the surface.

An excellent example of the holding back by peat of the water in a lake was related to me by a former student, after he had examined the above chart. A farmer living near his home had a peat bog with a very wide marginal zone and a low shore of considerable width. During dry years he was able to cultivate this ground with good returns, but during wet years he always lost his crop. Accordingly, in order to secure continuous use of his

[2] In the report in Science N.S. **29**:269, the height of the water above the surface should have been added, making a total of 113 cm.

land, he dug a ditch from the margin to the open water during the dry season of 1903. As soon as his ditch was opened, the water flowed from the open lake to the margin and he lost the use of the land entirely.

These examples show that there is very little movement of water in peat. The water may be several feet higher in one zone than in an adjacent one; the difference in height depends upon the nature of the peat. This fact is well known to persons traveling on northern bog areas.

The variations here shown to occur in the position of the water table in different zones during the summer and in the same zone during the season, bring very strong additional proof to the statements of DAVIS regarding the xerophytic structures of bog plants, which were quoted above in the discussion of bogs during a dry period of years. During the season the plants growing in these bogs are subjected to high water level in the spring, when the water table in all zones is approximately level with the open water of the lake. During the hottest and driest months of the summer the water supply is greatly reduced by a lowering of the water table, and when water is removed by the surface layers, it is very slowly replaced by that of the deeper parts. It is only in these surface layers that these plants root. In any bog where a clearing of any extent has been made, one finds areas where the tamaracks have been blown over during storms; these show that even the largest trees root in the surface layers only.

It has been shown in fig. 7 that the water table in the various parts of the bog stood at different heights during the summer. This is the controlling factor which makes the bogs in this region heterogeneous habitats, supporting xerophytes in three zones and hydrophytes or mesophytes in other zones.

The first effect of lowering the water table, as has been pointed out, is to make the habitat xerophytic, and one would expect that those areas where the water table is lowest would be most xerophytic. A glance at the plants shows that this is not the case; the outer zone in this lake is occupied by hydrophytes. This is due to secondary changes. Immediately after the water lowers, a number of other changes set in which produce the opposite

effect. With the decrease in the position of the water table, there is an increase in the oxygen supply, the number of soil organisms, and a rise in temperature. These produce a change in the composition of the peat, making water more and more available for plants and making the habitat less and less xerophytic. In older parts where this process has been going on for years, there is a decrease in the volume of the peat and a lowering of the surface. In the areas studied around Ann Arbor, this seems to be the explana-

FIG. 8.—Station under the tamaracks, showing *Chamaedaphne* almost entirely dead; the light value here was 0.033; photograph by STEELE.

tion of the marginal ditch characteristic of bogs there. In other areas different reasons have been given, but they do not seem to explain the condition found in this region (**16**). During wet periods the width of this ditch is often greatly increased, as has been pointed out previously. In such an area only those plants can grow which can stand high water during a term of wet years and high water during the spring of every year. The vegetation which is found here is much the same as that found under these conditions along the borders of our streams. The peat found

below the lowest level to which the water table gets in the driest times is red, while that above varies from red to brown and black. As has been pointed out, plants do not root in the red peat.

Humidity

Only a few readings were taken with some evaporimeters belonging to the Carnegie Institution and loaned by LIVINGSTON. The total evaporation for seven weeks was as follows: under tamaracks in sphagnum, 275 cc.; on floating sedge, 321.7 cc.; in an adjacent oak-hickory grove, 860 cc.; in an open field bordering the lake, 1056 cc. The last figure is short two days because the instrument was broken. These data, however, give conditions only near the surface, and are of value only in a study of germination in the different zones. It has been pointed out recently (**21**) that great variations are found in short distances above the surface in the amount of water lost by evaporimeters. A lack of instruments made it impossible to study this phase of the subject.

Light

Light readings were made with the usual form of photometer. It was found that the light falling upon the tallest plants in all zones was approximately the same. Great differences were found between these values and those light values found at the surface in the different zones. With light value in the open as 1, the following values were found: under *Chamaedaphne*, 0.0026; under tamaracks, 0.033; under brambles found in a clearing society where maple and cherry seedlings were found in large numbers and some few individuals of each had reached a height equal to the brambles, the light was only 0.00022; among the leaves of the brambles it was 0.166. The value 0.033 seems to be the minimum light requirement for *Chamaedaphne* in the region about Ann Arbor. Fig. 8 shows dead *Chamaedaphne* at First Sister Lake where the light value was 0.033.

The data recorded above show that the bogs of southern Michigan are for the most part not xerophytic habitats, but by far the largest areas are either hydrophytic or mesophytic. Only two or perhaps three of the zones can be considered as xerophytic habitats;

the two are bog shrub and tamarack. To these might be added, depending upon its width chiefly, the bog sedge. This conclusion is justified both by a study of the vegetation and the physical conditions. It is believed that the data furnished at least point strongly toward the supposition that these zones are today xerophytic habitats, even though they also prove that these same areas cannot long remain so. Numerous attempts have been made to explain the xerophytic structures in the plants found in these zones, but only slight reference need be made to them in this paper.

Some have regarded the peat bog as a hydrophytic habitat. Thus WHITFORD, after adding to other factors that of "insufficient aeration of the soil which prevents a healthy growth of the root system of land plants and also bars the presence of nitrifying bacteria," says that "these probably bring about xerophytic structures of plants so commonly seen in hydrophytic habitats." He quite correctly regarded the bog chiefly as a hydrophytic habitat. In the area in which he worked also the true bog plants were not as limited in their distribution as in southern Michigan. It is quite probable that other conditions would enter into a detailed study of bogs in the northern part of the state (**20**).

CLEMENTS (**6**) feels "that the current explanation of xerophytic bog plants, etc., is probably wrong, and that the discrepancy between the nature of the habitat and the structure of the plant is to be explained by the persistence of a fixed ancestral type."

SCHIMPER (**15**) attributes the xerophytic structures to the presence of humus acids in peat which impede absorption. LIVINGSTON (**12**) has shown that any effect produced by humus acids must be chemical, as "bog waters do not have an appreciable higher concentration of dissolved substances than do the streams and lakes of the same region." NILLSON attributes differences in structure between swamp and bog plants to a difference in food supply, but this will not hold in this area.

TRANSEAU believes from his observations and experiments that "in so far as southern Michigan is concerned (**18,** p. 36), the substratum temperatures prevailing in bog areas do not seem to be adequate to account for the presence or absence of bog plants

or their xerophilous structures. Experiments suggest, however, that farther north this factor is of prime importance"; again, on page 37, "an examination of all physical and chemical data now available fails to account for the differences in the flora of the bog and swamp areas of this region. The most important factor is believed to be the physiographic history. Where the habitat dates back to Pleistocene times and has remained undisturbed, we find today the bog flora. Where the habitat is of recent origin or has been recently disturbed, we find the swamp flora, or a mixture of bog and swamp species."

DACHNOWSKI (**7, 8**) believes from his experimental work that the condition which gives rise to xerophily and to zonation in bog plants "lies rather in the toxicity of the soil substratum, that is, in the production of unfavorable soil conditions brought about by the plants themselves." This author further says that "if water transpired is replaced by bog water," which would be the case to a limited extent during the summer when the water table was low and conditions for transpiration excellent, "the soils become more toxic." That is, the first effect of lowering the water table would tend to make the habitat more xerophytic. Further, "decrease in toxicity always follows aeration of the soil and drainage"; that is, an increased lowering of the water table admits oxygen, decreasing the toxicity of the soil and making the habitat less xerophytic. With this is also associated an addition of humus which increases the capacity of the soil "for the adsorption and retention of the toxins." If the results obtained by DACHNOWSKI are correctly explained by him as due to bog toxins, they do not conflict with the data recorded in this paper. It is to be hoped, however, that his studies will be pushed farther.

DAVIS, as has been pointed out earlier in this paper, believes that the bog is a xerophytic habitat, due to the drying of surface layers and the ability of peat to hold large amounts of water which are not available for the plants. The data given in this paper are in accordance with this view, and it appears to the author to more nearly cover conditions than any of the other theories advanced. It is not contradictory to the experimental work of the authors cited; this has been shown in the case of the work of DACHNOWSKI.

TRANSEAU suggested that in the regions farther north the temperature of the soil may be of prime importance. Temperature readings in deeper layers in the bogs of southern Michigan than those which he discusses, and yet not too deep for the root systems, resemble those of northern areas, and it is probable, in the light of his experiments, that they may be a controlling factor, even in those of southern Michigan.

YAPP (**21**), in his excellent paper dealing with the relation of marsh flora to evaporation, has shown that great variation exists in the amount of water that is evaporated by instruments placed at different heights above the surface. Hence two plants may grow side by side and yet not be under identical conditions. He produces a large amount of data, especially concerning factors affecting the aerial parts of plants. He concludes that "any argument drawn from mere proximity of position, without reference to the varying physiological problems of the different species, is entirely insufficient," and that "the arguments of authors, who insist that the so-called xerophytic structures of marsh plants can have no reference to present-day conditions, because both xerophytic and non-xerophytic species often grow side by side in nature, are entirely inconclusive."

Summary

1. The bogs around Ann Arbor are not xerophytic habitats, as such, but contain xerophytic, hydrophytic, and even mesophytic areas.

2. A study of the conditions in those areas which now are xerophytic indicates clearly that xerophytic conditions in bogs of southern Michigan will shortly disappear.

3. The presence of definite groups of plants in each zone is due chiefly to soil conditions found in that zone; also to position of the water table and secondary changes dependent thereon, as aeration, temperature, composition of the peat, etc.

4. The absence of certain plants from certain zones is due to decrease in the amount of light. *Chamaedaphne* apparently is not able to grow in this area in a light of 0.033.

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THE VEGETATION OF CRANBERRY ISLAND (OHIO) AND ITS RELATIONS TO THE SUBSTRATUM, TEMPERATURE, AND EVAPORATION. II

ALFRED DACHNOWSKI

(WITH ONE FIGURE)

The atmospheric influences as ecological conditions for growth

Various theories have been suggested to account for the presence and the relative persistence of this northern boreal flora under present climatic conditions. Some of these theories have been referred to earlier in the paper. Although widely separated from the central region of active bog formation with which the local bog is now only historically connected, its persistence and existence in spite of the climatic changes and animal and plant migration and invasion since the last glacial period, and the fact also that many peat deposits are reported to occur beyond the margin of the Wisconsin ice sheet, suggest that the most significant ecological factors are not to be looked for in the continuation of limiting conditions similar to those which prevailed when a colder climate existed than at present. That bog plants are related functionally as well as morphologically, and that they are grouped and localized with reference to more or less definite conditions of their environment is now a fact no longer questioned. It is also well known that no formation or plant society is likely to be relatively permanent and stationary, for there are changes constantly taking place in the environment as well as among the dominant plants and their associates. In the bog, however, but few successions of plants are in evidence, and the treatment of the vegetational societies from the standpoint of floristics and succession is therefore relatively free from complications. On the other hand, the determination of the factors in bog habitats, and the more detailed study of the dynamics of the process, that is, how some factors are related, their influence and duration—this phase of the problem is still in a state of uncertainty, and the methods of study have been all but satisfactory. When one con-

siders the bog as a habitat, the various causative and limiting factors entering into the plant environment are not so readily distinguished. In connection, therefore, with the analysis of the life conditions in bogs, associated also with the distribution of bog plants, and their conflict with species whose range is more southern, certain meteorological phenomena have been added below.

CLIMATIC CONDITIONS

One of the main objects kept in view during the progress of the investigation on the ecology of Buckeye Lake, and one which seemed to the writer an indispensable preface to both the field and the laboratory study, has been the climate of the region. The general statistics were taken from *Bulletin Q* of the U.S. Weather Bureau Service (**17**), and from manuscript to which access was had by the courtesy of Section Director HAYS of the Columbus (Ohio) Weather Bureau. No continuous series of climatological records have been made on Cranberry Island. The writer made records extending over the period of investigation; these records were supplemented by Mr. DICKEY, whose readings were taken each time the evaporation of the bog habitat was measured. It is felt that the comparative climate statistics given below are generalized data which do not lend themselves to investigation in physiological ecology. Though facing the same set of climatic factors, few of the species forming the flora of the bog island confront the same physiological problems, and hence any conclusions drawn from mere climatic data, without reference to the varying functional responses of the different species of plants, are certainly inadequate. However, the study of the meteorological observations is suggestive mainly in ascertaining the essential differences between the local region and the conditions found in the northern center of bog formation, and in estimating the average temperature and humidity exposure of the plants. The data given in table IV are for Columbus, Ohio; for Ann Arbor, Michigan, where bogs and swamp-lands are found more abundantly; and for Marquette, Michigan, where this type of vegetation reaches a still higher development.

TABLE IV

GENERAL METEOROLOGICAL CONDITIONS

	Columbus, Ohio	Ann Arbor, Mich.	Marquette, Mich.
Elevation	774 ft.	930 ft.	668 ft.
Years of record	31 yrs.	25 yrs.	33 yrs.
Mean seasonal temperature in degrees F.			
Winter	31	26	19
Spring	51	46	37
Summer	73	70	63
Autumn	54	51	45
Annual mean	52	48	41
Absolute maximum	104	101	108
Absolute minimum	−20	−24	−27
Absolute range	124	125	135
Greatest annual range	118		124
Least annual range	89		97
Frost, aver. date of last in spring	April 16	April 28	May 15
Frost, aver. date of first in autumn	Oct. 16	Oct. 9	Oct. 2
No. of days in growing season	176	157	140
Mean seasonal precipitation in inches			
Winter	8.9	6.6	6.1
Spring	10	7.9	7.3
Summer	10.3	10.1	9.4
Autumn	8	7.6	9.6
Annual mean	37.2	32.2	32.4
Absolute maximum	51.2	47.7	42.9
Absolute minimum	26.4	21.1	25.3
Mean annual relative humidity	79	79	80
No. days precipitation	144	138	161
Aver. direction of prevailing wind	S.W.	S.W.	N.W.
Aver. minimum wind velocity	48 miles	.....	46 miles

From the data in table IV, it will be observed that the seasonal and annual temperature decreases as one travels from the southern limit toward the northern center of bog vegetation. The climate of the region about Columbus is characterized by a milder winter but a relatively hot summer. The annual range in temperature is comparatively smaller than at Marquette, 102° F. as against 112° F. The normal annual range is here only between 96° F. (35°.5 C.) and −6° F. (−21°.11 C.), and the greatest departure from the normal variation does not exceed 16° F. The monthly averages for only two months are at Columbus below 32° F. (0° C.), as against five months for Marquette. The normal number of days per annum with a temperature above 43° F. (6° C.), the factor upon which SCHIMPER (**29**) and MERRIAM (**27**) base the boreal limit, is at Columbus approximately 185, that is about one-half of the year, as against 122 days at Marquette. The

normal sum total of effective daily temperatures above 43° F. (6° C.), the estimate for which is derived by multiplying the mean average monthly minimum temperature of that period by the number of days, is 10414° F. (2520° C.), as against 6466° F. (1422° C.) for Marquette. The normal mean temperature of the six consecutive hottest weeks of the year, effective also in determining the austral limit of species, is 75°. The warmest month is July with an average monthly maximum of 86° F. (30° C.), as contrasted with 77° F. (25°C.) at Marquette. The coldest months are January and February with an average monthly minimum of 22° F. and 23° F. (5° and 5°.5 C.) respectively, as contrasted with 10° F. and 9° F. (12°.5 and 12°.0 C.) respectively for Marquette. The dates of the latest killing frost in spring and the earliest in autumn, although not the exact limits of physiological activity in plants, or the limits of the growing period of most plants, are nevertheless an unquestionably important factor. Six months of the year are normally free from frost about Columbus.

Though the relation between rainfall and the amount of water needed by plants is of great importance in regard to differences in vegetation, the rainfall and its distribution during the seasons, and the number of rainy days, are of greater significance than is the amount of rain. At Columbus precipitation is quite evenly distributed, reaching an optimum of 10.5 inches (26 cm.) during spring and summer, when the vegetative functions of bog plants are more active, with a minimum of 8.5 inches (21 cm.) during the season of low temperature and in the quiescent period of plants. Columbus exceeds the annual precipitation at Marquette by 4.7 inches (11.8 cm.); the average number of days with rainfall during the year, however, is considerably less than in northern Michigan, 144 days as against 161 days. In the north the greater precipitation is in the form of snow. Marquette has over five times more snow than Columbus, 125.7 inches (315 cm.), as contrasted with 23.5 inches (59 cm.) here. In this vicinity the longer growing season of the plants has therefore correspondingly more of the precipitation available. On account of the higher temperature more moisture is needed, and hence the evaporation also is much greater here than at Marquette. Cold air does

not take up so much water as does hot air; consequently the additional amount of water which the atmosphere is capable of taking up to become saturated, that is, the evaporating power of the air, is greater here than at Marquette. The amount of evaporation also depends upon several other factors and conditions; the values of these will be taken into consideration below. Where evaporation is nearly as great as precipitation, the seasonal distribution of rainfall and humidity is a matter of greatest importance, for it is known that scanty rainfall throughout the year, or relative dryness of air and soil during the growing season, favors the development of xerophytic forms in almost any region. The relative humidity of Columbus and vicinity is only slightly less when compared with the north, the percentage of saturation ranging from 79 to 80 respectively. The distribution varies during the year only to a small extent between the month of least and that of greatest normal humidity.

The rate of movement of air currents is, no doubt, of great importance to vegetation, not only because of the direct mechanical effect and the indirect physiological action in increasing the evaporating power of the air, but also because transpiration increases with the velocity of the wind. That wind is an ecological factor of the greatest importance has been emphasized by many authors. KIHLMAN and WARMING regard xerophytic structures in plants as acquired and necessary, on account of strong drying winds in exposed places. Even humid atmosphere when continually renewed leads to strong transpiration, and the danger may be decreased only as protection is provided either through density and height of species, or admixture of a variety of species in a community of plants. The average maximum velocity of wind does not vary greatly between Columbus and Marquette, and hence the influence of wind, though considerable in more exposed places, has apparently little relation to the differences to be accounted for in the character of the local vegetation.

Briefly summarized, the region about Columbus and Buckeye Lake is characterized by a longer growing period with a relatively higher sum total of temperature exposure, a milder winter with normally slight variations, well distributed rainfall, and a relatively

high percentage of atmospheric humidity. The local climáte is therefore preeminently a deciduous forest climate. The whole region was in its recent primitive condition densely forested. On the other hand, the marked increase of bog development in area and in variety of species in northern localities seems to be correlated with a decline in extremes of summer temperatures and an increase in relative humidity. The general effect is to produce a balanced functional relation, though limited in range, between the amounts of water absorbed and transpired. This phenomenon associated with bog habitats will be discussed in connection with a further analysis of the life conditions obtained in bogs from the point of view of their physiological aridity.

If we take the above mentioned climatic factors into account in the interpretation of local bog conditions, it will be seen that meteorological data in this region are not such as to produce or account for xerophily or for persistence of bog floras. The climatic changes by which a region varies, if severe and varying between wide diurnal and seasonal changes in temperature, humidity, and light, entail naturally modifications in the functions and in the composition of a flora. The vegetation would be tested to the limits of its power of adjustment and acclimatization, and only the forms which had a greater efficiency of responses and had powers of resistance intensified to a new place-function would take up the habitat to the extent in which survival under the modified conditions would be possible. It has been pointed out above that changes in the flora are now occurring and have occurred during the development of the bog island. Many of the former plants have disappeared and are no longer to be found here, while others have survived, hold tenaciously the area under control, and are still constituents of the present flora. Their preservation in this region would seem to be dependent upon less obvious factors than climate. Functional habitat relations, as well as such ecological life relations as are comprised in association, in ecesis, and succession, need therefore the more detailed investigation. In determining these the first component to be considered is the rôle of low substratum temperature. The temperature of a soil is a phytogeographical factor of great significance, but its weightiest

importance is in its effect upon the functional activities of roots and rhizomes. Recently the temperature of soils and its fluctuations have received considerable attention. The relationship, however, and the general effect upon plant forms and the correlated functioning are nevertheless but little understood. This circumstance is perhaps the more to be regretted, since, broadly speaking, it seems that the relationship to plant life is the more favorable the more dominating the influence of the physical characters of the soil and particularly the relations prevailing in regard to the physiological water content and efficient temperature.

THE RÔLE OF SUBSTRATUM TEMPERATURE IN BOG HABITATS

During the first few months of field work the device chosen for obtaining the substratum temperatures was the "thermophone." The apparatus is based upon the principle that the resistance of an electric conductor changes with its temperature. In obtaining the temperature of peat soils at various depths, the coils were sunk to the required depth, and their leading wires were then connected with the respective binding posts of the indicator box. A buzzing sound in the telephone increases or diminishes according to the position of the pointer while receding from or approaching to a section of the graded dial. Hence the position is soon found where the telephone is silent. This point indicates the temperature of the sunken soil. The instrument is very sensitive, but very inconvenient for obtaining weekly and monthly minimum and maximum temperatures. Later in the season the investigations were planned for a set of thermographs such as MacDougal described (**25**), that would make a continuous record of the temperatures at any desired depth. The lack of sufficient funds and the failure to secure similar instruments made it necessary to resort to a conventional though less graphic method of measuring the temperature exposure of plants. In the field work of 1908, 1909, and at present, mercurial minimum and maximum thermometers were therefore used. The thermometers for the deeper peat strata were fastened to wooden poles and pushed down into the soil to the depth of 5 feet (1.5 m.). They remained in the soil during the period of investigation except for such short

periods of time as were necessary to make a reading. For strata nearer the surface differential and ordinary mercurial thermometers were used, the bulbs of which were pushed down into the peat around the rhizomes of the plants to a depth of one foot (20 cm.) and three inches (7.5 cm.), respectively. The glass stems of the exposed instruments remained shaded from the direct rays of light. The temperatures recorded below, in centigrade, were generally taken on afternoons, usually between 12 and 2 P.M. It should be kept in mind that the maple-alder zone conditions correspond very nearly to those of the tamarack-willow-poplar zone of the northern bogs and swamps, and that a similar relation exists between the local central zone and the open bog-sedge zone of northern bogs.

The readings taken during the period of observation are too voluminous for a tabulated record. Only those of the seasons of 1909 will be given in this place (table V).

TABLE V

TEMPERATURES (C.) IN THE PEAT SUBSTRATUM OF CRANBERRY ISLAND SEASON OF 1909

Station	Jan. 12	Feb. 26	Mar. 29	Apr. 23	May 14	June 11	July 17	Aug. 14	Sept. 11	Oct. 2	Nov. 30	Dec. 28
Central (sphagnum-cranberry) zone:												
Air 1.5 m.	0.5	5	14	23.5	24	26	24	28	27	17.5	14	3.5
Air 30 cm.	0.5	4.5	14	24	25	26	24	28	27	17	14	2.5
Air 7.5 cm.	1.0	4.5	14.5	22	26	29	24.5	28	27.5	17	14	2.5
Soil 7.5 cm.	0.5	1.5	10	12	14.5	21.5	24	25	22.5	16	7	0.5
Soil 30 cm.	0.5	2.0	7	10.5	12	21.0	24	25	22.5	17	8	2.5
Soil 1.5 m.	7.5	6.3	8.5	9	11	16.0	21	22	22.5	21.5	16.5	13.0
Maple-alder zone:												
Soil 7.5 cm.	0.5	1	11	11	16	20	20.5	22	20	14	8	4
Soil 30 m.	1.5	2.0	9.5	10	14	19.5	21	21.5	20	15.5	9	9.5
Soil 1.5 m.	6.5	5.0	8.0	10.5	14	17.5	19.5	21.5	21	19	15.5	14
Lake zone:												
Water 7.5 cm.	1.5	1	13.5	14.5	20.5	26	29	28.5	25	15	6.5	3.5
Water 30 cm.	1.5	0.5	13.5	14.5	20	26	29	28.5	25	15	6.5	4
Water 1.5 m.	1.1	2.7	13	13.8	18.8	22.5	26	26	24	12	6.5	5

A glance at table V shows that the temperature conditions, though comparatively uniform and high throughout the bog island, range somewhat lower in the maple-alder zone than in the central

zone. There is a large daily as well as annual range in temperature, but the range is considerably less in the soil than in the air above. The data obtained are sufficient to strengthen the observation made, that in the spring the ice in the central zone melts with greater rapidity, and that a higher temperature results from the greater insolation and the increased absorption and retention of heat rays. On days following a sudden lowering of the air temperature, and also on cloudy days, the temperature of the surface bog water and bog soil in the sphagnum-covered area stands above that of the maple-alder zone. This gain in temperature is cumulative and aids in the penetration of heat rays below the surface. The heat supply is obviously the most direct factor contributing to the substratum temperature, for the variations are associated directly with the amount and intensity of sunshine. The extreme slowness in the maple-alder zone is explained partly by the low conductivity of the partially decayed peat and the lack of a free circulation of air above the soil, but largely by the increasing diffusion of light rays due to the leafing out of trees and shrubs.

Another point of interest is the fact that notable differences are found between the temperatures of the bog island and the surrounding lake water. When we compare the effects of gain and loss of heat between the free water surface of the lake and that of the peat area clothed with vegetation, it will be seen that the temperature of the central and the maple-alder zone remains higher than that of the lake during the autumn and winter months, and that during spring and summer the lake water is warmer at the respective (1.5 m.) depths than the peat substratum. Water has a specific heat far greater than any soil; it retains its heat longer and for this reason is warmer than the peat substratum in spring and summer. On the other hand, peat and humus are cooled more rapidly at the surface by the evaporation of water during the warm days of the seasons. The values of both heat conductivity and diffusion are in general lower in peat than in water, and hence a rapid loss of temperature in the peat strata below the surface vegetation is thus prevented.

A high temperature phenomenon existing in certain places is worthy of special mention. Not infrequently small sheltered

areas are found in the central zone bordering the *Rhus-Alnus* thickets where ice never forms in winter. Such temperature conditions would not attract special attention were it not for the fact that usually the temperature is so much lower in the adjacent areas. From a biological standpoint this fact is significant because these conditions favor isolation of habitats and produce a prominent floristic difference. *Wolfiella floridana* commonly occurs in these "warm" pools.

Plants are not dependent so much upon the mean annual temperatures as upon the minima and maxima of temperature encountered, and upon the duration of the vegetation season. To throw some light on the characteristic temperature range occurring throughout the year and within a growing season, the temperature data of the monthly extremes for the seasons of 1908, 1909, and for the autumn and winter of 1907, and the spring of 1910 are appended. As far as the writer is aware, no observations of minima and maxima temperature records within a bog, covering a period of three years, have been carried out thus far. On account of the fact that the present data were obtained at a station whose ecological significance is especially interesting, table VI of the temperature data is deemed worthy of a closer consideration.

We see again that the temperature of the substrata at the different levels is affected less by the alternate heating and cooling at the surface, but in a far greater degree by the progression of the seasons. It increases slowly during May, is stationary more or less during August and September, and begins to decrease fairly rapidly in November. The maximum temperature occurs in July and August, and the minimum temperature is registered in January for the central zone. That of the maple-alder zone occurs in February. Observations have shown that the lake freezes to a depth of 8–15 inches (20–37 cm.), while the bog is covered by ice to a thickness varying from 3 to 5 inches (7.5–12.5 cm.), except for a few places where ice never forms. Consequently, the strata in the bog area below the one-foot level (30 cm.) are well protected from lower temperatures and from sudden temperature changes. When the sun's heat melts the ice and snow, the percolating water derived from the melting ice lowers the temperature of the deeper

strata a few degrees in the early spring. The wave of temperature increase falls here slightly behind in March, but the upper strata are not prevented from rising in the meanwhile rapidly above the freezing point. Though of ecological importance as a protective cover during the winter months, and of significance as a bad conductor of heat and in decreasing fluctuations in temperature, the ice and snow do not, therefore, retard appreciably the beginning of favorable growth conditions. The maples and willows of the

TABLE VI

MINIMUM AND MAXIMUM TEMPERATURES IN THE CENTRAL ZONE AT CRANBERRY ISLAND, 1907 to 1910

	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
Air:												
Max.....	18.3	15	25	27.2	31.6	33.3	35	35	34.5	30	23.3	19
Min.....	−19.4	−24.5	−8.8	−7.7	0.5	3.3	8.3	7.2	−1.6	−5.5	−9.4	−21.6
Range....	37.7	39.5	33.8	34.9	31.1	30.0	26.7	27.8	36.1	35.5	32.7	40.6
Soil:												
1 ft.(0.3 m.)												
Max.....	4.5	3.3	9	13.3	15	25	27	25.5	25	17.7	13	9
Min.....	0	1.2	0	6.6	10	18	17	21.	16	12.5	8	2.5
Range	4.5	2.1	9	6.7	5	7	10	4.5	9	5.2	5	6.5
Soil:												
5 ft.(1.5 m.)												
Max.....	13.3	9.2	9	12.2	12.5	17	23	26	22.5	22	20	15.5
Min.....	7.5	3.9	4	7.2	9.5	14	16	22	20	18	16.5	13
Range....	5.8	5.3	5	5	3	3	7	4	2.5	4	3.5	2.5

GREATEST RANGE

Air: max. 35; min. −24.5; range 59.5.
Soil 1 ft. (0.3 m.): max. 27; min. 0; range 27.
Soil 5 ft. (1.5 m.): max. 26; min. 3.9; range 22.1.

bog island are in flower about 8 to 10 days later than those on the campus of the university. A persistence, however, in the peat substratum of the winter cold and ice through the summer months is not proved, at least in this region. The records taken at a depth of 5 feet (1.5 m.) below the surface vegetation show a variation in temperature between 3°.9 C. and 26° C., i.e., an annual range within 22° C. At this depth only the anaerobic bacterial bog flora is most active. The roots and rhizomes of bog plants do not penetrate beyond the depth of 2 feet (0.6 m.), and the roots of

maples still less. Plants imbedded in the peat at a depth of 1 foot (0.3 m.) are within ranges of temperature from 0° C. to 27° C. The underground growth of the plants continues when the winter temperature in the substratum rises and reaches the gradient from 4° to 8° C. When these soil temperatures prevail during winter for a sufficient length of time, the different stems and buds shoot upward and develop leaves and lengthen their internodes rapidly in the warmer weather of spring. The absorbing organs at 3 inches (7.5 cm.) depth in the peat substratum encounter a mean average of 13°.5 C. with an amplitude of more than 30°. In all cases, however, the range of temperature in the maple-alder zone is less than that of the central zone by a difference of at least 6°.

These observations and facts disclosed as to the actual temperatures in the peat substratum of Cranberry Island, and the seasonal changes therein point to the following conclusions:

1. The soil temperature of two plant associations formed about the bog island are slightly different, and each association has its own characteristic temperature range.

2. Of the two plant associations in the bog area, the one more liable to extreme low temperatures in the spring and during the growing season is the maple-alder zone along the border of the lake, and not the more xerophytic central zone.

3. The substratum temperatures as phenomena of the local peat deposits are not favorable to the preservation of bog types, if low temperature is considered to be an edaphic criterion; in connection, therefore, with an analysis of the life conditions in this bog area low temperature is not a limiting factor.

4. A persistence of the winter cold and ice through the summer months is a point not proved either by observation or by registering instruments. The persistence of northern forms in this bog, therefore, has some other cause than low temperature of the substratum. In arctic latitudes, no doubt the most significant factor in determining the character and the distribution of plants, as well as in the formation and preservation of humus material, is low temperature. In the latitudes of Ohio, temperature is not a factor in the process. Neither does the accumulation of humus finally bring about edaphic conditions "too cold and too acid."

5. It is not low temperature that kills invading mesophytes, but the edaphic physiological aridity prevailing in the central zone, which decreases the absorption of water by roots at a time when transpiration and the growth of the plants demand a greater physiological soil-water content.

6. The topographical distribution of plants in the bog is also affected by relations in regard not to low temperatures, but to the uneven physiological water content and the physical condition in the peat substratum.

THE DIFFERENCES BETWEEN AIR AND SOIL TEMPERATURES

We proceed now to a brief consideration of the question whether the differences between air temperature and that of the soil are sufficiently marked during the growing period to prove a factor in the selection of plants for bog areas. To show this relation, data on the corresponding minimum and maximum air temperatures for the period under investigation have been added to table VI. The records were taken from the Climatological Service of the U.S. Weather Bureau at Pataskala, some 35 miles (0.56 km.) distant from Buckeye Lake. They represent fairly nearly the conditions at Cranberry Island on the corresponding period. Additional data are found also in table VIII. Upon comparison it will be seen that during July and August, the months which proved most critical for the cultivated plants grown in the bog area for experimental purposes, the shoots of plants were in an atmosphere varying between 7° and 35° C., while the roots and rhizomes were at temperatures varying between 16° and 27° C., i.e., within a range of temperature differences not less than 9° and not more than 19° C. For a growing season lasting from May 5 to October 1, the average date of the latest and earliest killing frost, the actual differences between the temperature of shoots and roots amounted to 34°.5 and 21° C. for each of the absorbing and transpiring organs respectively in the central zone, i.e., within a range of 29° C. It is seen that rapid and passing changes of air temperatures and the occasional extremes do not affect the substratum temperatures. Only average effects prevail and the

great periodic seasonal changes. In winter and in summer the minimum temperature of the peat substratum is considerably higher than that of the air. Consequently, the annual mean temperature of the soil greatly exceeds that of the air. The monthly and annual fluctuations of temperature affect the peat area to a depth of 2 m., but they are at no time greater or with a wider range than those of the air. At what depth the mean temperature would remain constant has not been determined.

That the differences between the temperatures of the air and that of the substratum are not as great as is generally supposed, is a fact upon which it is needless to elaborate further. They cannot be looked upon as factors in bog development or in the characteristic xerophily of the sphagnum-covered area in this region, and hence neither the substratum temperature nor the differences between soil and air temperature are of sufficient importance to enter into the problem of bog flora, and zonation or ecesis and succession. The records show that on the basis of temperature as the initial factor the central zone conditions are somewhat more rigorous, and that these conditions are mitigated in the maple-alder zone; but it cannot be claimed that the differences of the plant covering in the two zones are directly correlated with the differences of temperature. With no attempt to minimize its influence, it is evident that for a comparison of habitats, temperature, at least as a single physical factor, is a matter of very subordinate importance on which to establish a causal relation. Those factors acting in conjunction with it demand the greater emphasis. It is questioned, therefore, even for regions where bogs reach their optimum development, whether the coefficient of the differences between the soil and air temperatures is to be looked upon as having a greater value than here in the selection of plants for bog areas, or the production of xerophilous characters.

Whether or not important correlations between the temperature differences and the transpiratory activities of bog and other plants may be expected, a study of the transpiration quantities will doubtless reveal. Work of this character is now in progress and will be published as soon as opportunity permits.

THE RÔLE OF THE EVAPORATING POWER OF AIR

As a preliminary study to the transpiration value of bog plants and to the question also whether the xerophytism and the stunted growth so manifest on maples, poison sumach, and various other plants in the central zone is brought about by an excessive evaporating power of the air, quantitative measurements have been made by the volumetric method to determine the saturation deficiency of the air in three representative stations.

Evaporation is one of the most important factors of the meteorological cycle of a locality. To the student of agriculture and of plant physiology it is a problem the study of which aids in supplying much of the desired information on the growth of plants in irrigated and uncultivated fields. HANN (**16**), who studied evaporation chiefly from the point of view of the meteorologist, has pointed out that the amount of water which the atmosphere is capable of taking up to become saturated is one of the indices of the influence of climate. The highly important observations made by LIVINGSTON (**21, 23**) emphasize the fact that the effect of an atmosphere of great evaporating power undoubtedly influences the geographical distribution of plants, and through its local variations exerts an equally determining effect as a physiological and an ecological factor. The problem of evaporation has been but imperfectly appreciated, and though the bibliography of evaporation is extensive (**24**), the correlation between the evaporation under different conditions has not been satisfactorily formulated. The evaporating power of the air is generally understood to comprise a resultant of temperature, humidity, and wind. But evaporation is very sensitive to soil as well as to air relations, and since a multitude of local factors may influence either of the two conditions, the amount of evaporation integrates the effect of numerous variables. Evaporation is a rather complex resultant, therefore, and in preparing for an investigation which has in view the measurement of the amount of evaporation in plant societies, it is important to keep in mind the several conditions entering into the problem. It is necessary to recognize that the essential details of the phenomenon of evaporation are different in the great variety of conditions, and require separate and special study

appropriate to the peculiar conditions. To measure evaporation in a few places in this locality, and then to assign the results to the region as a whole, is a procedure not without its accompanying shortcomings. It was intended to overcome this difficulty partially by measuring the variation in evaporation of the vertical as well as the horizontal vapor pressure gradient in a larger number of stations, plotting the results, and drawing isothymes. By a summation of the evaporation, that of the whole area could be calculated with greater accuracy. The distance of Buckeye Lake from Columbus and the inconveniences as to available time have made it difficult to secure the required observations. However, the problem here dealt with does not concern itself with the development of a formulated expression of evaporation for this region. The purpose at present is to obtain quantitative data on the rate of evaporation, and thus to secure direct evidence as to the relation of the observed evaporating power of the air and the nature of the vegetation. The more detailed study of the phenomenon as originally outlined is now in progress.

The ordinary markets are not prepared to supply the well designed standardized self-registering instruments which have been devised to meet the needs of the Weather Bureau (**26**). For ecological purposes, an instrument is required which can be placed under conditions practically identical with those which the plants themselves endure. For this purpose a small atmometer partly buried in the soil is desirable. Dr. FORREST SHREVE of the Carnegie Desert Laboratory, Tucson, Arizona, courteously left at the disposal of the writer several porous cups of the type as described and used by LIVINGSTON (**21**). The instruments had been previously standardized with an atmometer at Tucson, and since they are similar to those sent out from the Desert Laboratory to various other stations in the United States, the readings obtained may be readily compared. There are certain objections to the porous cups as an instrument in the field study of habitat conditions. The inability of the cup to withstand frost makes it practically impossible to obtain readings for more than the growing period of seven months, and the fact that the instrument does not prevent the direct entrance of rain to the jar

introduces an error which becomes very large as the time interval between the reading of the instruments and the length of time and the amount of precipitation increases. The instrument recently described by YAPP (**34**) and by LIVINGSTON eliminates the error last mentioned, but some weighing method, when available, will probably be more exact than any, since it alone can be employed in the measurement of evaporation from ice, snow, and growing vegetation.

Of the instruments on hand, one was established as a standard in an open lawn freely exposed to the sun and wind on the campus near the University Observatory. It was placed in a manner to obtain readings on the saturation deficiency of the air at a height of 15 cm. above the soil surface. The atmometer remained in the care of Professor H. C. LORD and his assistant Mr. KENDRIG, to whom the writer expresses his warmest thanks for their helpful interest. The records were taken three times daily in connection with the climatological observations called for by the U.S. Weather Bureau Service, and consisted of the reading of the depth of water remaining in a graduated container. The instrument continued in operation from May 21 to September 17, when an accident resulted in the breaking of the graduated retainer. Within a few days the trouble had been remedied and the observations proceeded until October 11, when the first heavy frost occurred.

Another cup was placed in an open and exposed place in the cranberry-sphagnum (central) zone, under conditions similar to those of the standard instrument. It was installed May 14. With the exception of the period from June 11 to July 17, when the total for five weeks was recorded, the loss of water by evaporation was determined at intervals of one week by running in distilled water from a graduate, thus restoring the original water level of the container. Records were obtained until August 21, when it was found that the atmometer had been disturbed. A week later it had disappeared entirely. No attempt was made to replace it by another.

The third instrument stood in the shaded conditions of the maple-alder zone. It was placed near large-sized maples whose cover was relatively dense though open. The reading of this

instrument extended uninterruptedly to October 2. During the writer's absence in Europe, the readings in the two plant zones were recorded by Mr. DICKEY; they have since appeared in published form (**12**). It is not necessary to reproduce in detail the original observations for the entire period. A series of data from the observations made have been summarized here and the conclusions stated.

Following are the atmometer readings for the several habitats, together with the comparative evaporation expressed in percentage of the standard instrument (table VII).

TABLE VII

ATMOMETER READINGS FOR STATIONS ON CRANBERRY ISLAND AND THE UNIVERSITY CAMPUS

1909 week ending	University station	Central, sphagnum-cranberry zone	Percent. diff.	Maple-alder zone	Percent. diff.
May 28	118.8 cc.	97 cc.	81.6	78.1 cc.	65.7
June 4	110.9	92.1	83	60.5	54.5
June 11	88.1	53.3	60.5	27.5	31.2
Five weeks ending July 17	487	349.2	71.7	290.4	59.6
Week ending July 24	151.4	120.2	79.3	77	50
July 31	117.8	69.8	59.2	50.6	42.9
Aug. 7	140.6	69.8	49.6	36.3	25.8
Aug. 14	134.6	82.4	61.2	70.4	52.3
Total evaporation	1349.2	933.8	69.2	690.8	51.2

As was to be expected, by far the smaller part of the total evaporation on Cranberry Island occurred in the maple-alder zone. The annual evaporation within the maple-alder zone is now about three-fourths of that in the open central zone, that is, fully 25 per cent of the moisture is saved by shade-producing trees and shrubs. The evaporation within this zone is greatest in the season from October to May. The difference in evaporation between this zone and the central zone is then at a minimum, but later it follows closely the growth of the leaves in the early spring and their fall in autumn. The maximum difference occurs in June and July. As the seasons advance, the evaporating power of the air in the forested zone varies with precipitation. Wind

and temperature are less effective, for as the leafing out of the trees proceeds, and the increased undergrowth also becomes effective in shade and interference with air currents, the retention of the moisture in the air decreases the evaporation rate and the relative humidity is raised. It would be instructive to follow in more detail the effect of the various meteorological factors on evaporation. This effect can very well be seen if the more important factors like temperature, intensity and duration of light, precipitation, wind, soil, and vegetation are referred to individually. But the results are uncertain and suggest the desirability of preliminary investigations in artificially maintained conditions by laboratory methods. In a general way, however, the data show that the inner temperatures of the maple-alder zone are lowered and the temperature extremes moderated, but the extremes in summer temperature much more so than those of the winter. The range in temperature is therefore more affected than the absolute temperatures. The importance of shade producers does not consist alone in their effectiveness to reduce transpiration, but also in their inverse influence upon meteorological factors.

The foregoing table also shows that the greater saturation deficiency was recorded for the station on the university campus. The relative evaporation in the three stations is according to the totals 1349.2 cc., 933.8 cc., and 690.8 cc., the corresponding ratios are 100, 69.2, and 51.2. These differences for the three stations remained fairly constant throughout. The fact that the evaporation rate for the central zone with its numerous xerophytes should be less than that for an area which supports mesophytic forest trees seems anomalous and surprising. Thus for the vegetation on the university campus the furtherance of transpiration by the evaporating power of the air is during some periods approximately two times greater than that on Cranberry Island. This clearly shows that the evaporating power of the air, though furnishing a very valuable criterion for the differentiation between great centers of plant distribution and for the differentiation of habitats, is not an important factor in controlling bog vegetation or determining the character of it.

With the data on hand, it is not difficult to see that the chief

TABLE VIII

VERTICAL EVAPORATION GRADIENT IN THE CRANBERRY-SPHAGNUM ZONE, CRANBERRY ISLAND

Date	Time	Light*	Anemometer; velocity in miles	Evaporation in cc.: cup at 3 in. (7.5 cm.) above ground	Temperature (C.); absolute, min.	max.	range	Evaporation in cc.: cup at 1 ft. (0.3 m.) above ground	Temperature (C.); absolute, min.	max.	range	Evaporation in cc.: cup at 5 ft. (1.5 m.) above ground	Temperature; absolute, min.	max.	range
July 30...	6 A.M.	sky clear	34.1	4.86	20	38	18	6.64	20	28	8	9.96	22.5	28	5.5
	12 M.	2 sec.													
	6 P.M.		25.1	11.34	21	37	16	14.94	24	32	8	19.92	26.5	29	2.5
July 31...	6 A.M.		3.6	0.00	8.5	27	18.5	0.00	8.5	27	18.5	1.66	11	28	17
July 31...	12 M.	8–9 sec.	18.1	3.24	16	34	18	6.64	18	30.5	12.5	9.13	17	27	10
July 31...	6 P.M.		12.7	6.48	22	42.5	20.5	7.47	21	30.5	9.5	10.37	24.5	28	3.5
Aug. 1...	6 A.M.		5.6	0.00	8	22	14	1.66	8	21	13	4.56	10.5	23.5	13
Aug. 1...	12 M.	7 sec.	12.1	4.05	15.5	35.5	20	6.64	18.5	32	13.5	7.47	16.5	28	11.5
Aug. 1...	6 P.M.		12	8.91	24.5	37	12.5	9.96	23.5	33.5	10	12.45	25.5	31.5	6
Aug. 2...	6 A.M.	sky clouded	5.4	0.00	13.5	24.5	11	0.00	13	23.5	10.5	2.49	11	31.5	20.5
Aug. 2...	12 M.	28 sec.	23.9	4.81	19	33.5	14.5	7.47	23	31	8	9.96	11	29.5	18.5
Aug. 2...	6 P.M.		25.7	5.67	25	34.5	9.5	7.47	24	32	8	10.19	25	30	5
Aug. 3...	6 P.M.	cloudy	85.1	14.58	19	37	18	21.58	15	37	22	28.22	17	35	18
Total evaporation				63.94				90.47				126.38			

* Time exposure at noon for sensitive photographic paper to standard tint.

external factor which exerts a direct influence on the evaporation at the bog island is the water area surrounding the island. Evaporation from the water surface and from the vegetation produces a vapor blanket, the action of which influences to a great extent the normal range of evaporation under the varying temperature conditions and consequently the rate of transpiration. The evaporation blanket is readily transported over the open central zone, its rate of movement and consequently the rate of evaporation varying particularly with the action of the wind. In the relatively forested maple-alder zone, however, the vapor blanket is more stationary and hence more uniform in its influence. This vapor blanket covers the locality to a definite height vertically. Studies on the phenomena of evaporation of water over lakes and reservoirs (**3**) have shown that the vapor pressure of the vertical gradient varies, beginning nearest the evaporating surface with a maximum, and rapidly diminishing within several feet above the evaporating surface, until it approximates to that in the free air. A few isolated readings confirmed this for the stations in question, as table VIII will show. At first the readings were taken every hour from 6 A.M. to 6 P.M.; later at intervals of six hours. For convenience, the larger time values covering the period from July 30 to August 3 are given here (fig. 8). The amounts are in the ratios 100, 71, and 50 for positions at 5 feet (1.5 m.), 1 foot (0.3 m.), and 3 inches (7.5 cm.), respectively. Hence in general, the lower stratum of a vegetation has a smaller range in humidity variations and possesses an atmosphere usually much more humid than the upper vegetation stratum or the free air above the vegetation level. The data confirm the noteworthy results of the evaporation experiments by YAPP (**34**), and show that the bog vegetation at the lower levels is exposed to transpiration conditions much less severe than those existing at positions above the substratum and those quite clear of vegetation.

But the growth of bog plants and their successful occupation of the habitat do not depend so much upon the total amount of evaporation or the time factor of this exposure, that is, the amount of moisture which the air contains during critical periods of the growing season. The functional activity of the plants is

not one of relation to a single factor. In the interrelation of conditions, the real limiting factor to an increase in functional activity is not evaporation or temperature, but the toxicity of the substratum. This fact reveals itself only in experimental tests. Toxicity comes markedly into play when the amount of water available for absorption has reached a stationary value, through

FIG. 8.—Experiment station in the cranberry-sphagnum association; in the foreground stunted growth of *Rhus Vernix;* photographed July 31, 1910.

the activity of bacterial organisms and other processes. In the field it is very difficult at times to decide which features of the vegetation are to be correlated with low atmospheric humidity, which with variations in temperature and light conditions, or with other factors cooperating at the same time. It is obvious that each in its turn may play the part of a limiting factor, for growth and transpiration are very susceptible to variations in either of these conditions. But in the laboratory the extended experi-

ments with cereals, legumes, and with plants from the various zones of the island have shown that most plants are unable to provide for a balanced relation between the supply of physiological water which the bog substratum can furnish and the excess of water lost during transpiration even when the temperature or the evaporating power of the air are favorable for any length of time. The susceptibility of the plants to the presence of small traces of deleterious bacterial transformation products accumulating in the surface layers of the peat substratum has been demonstrated elsewhere. An intimate and controlling relation has been found to exist between soil bacteria and the plants growing in the central zone. This has shown itself by various physiological and chemical tests, and by the fact that the presence and fitness of bog plants in the central zone is due mainly to more efficient functional responses to physiological drought. The edaphic aridity prevailing in this zone decreases the absorption of water by the roots in wheat plants about 50–65 per cent, at a time when transpiration and the growth of the plants demand a greater physiological water content. The further quotation of definite examples must be postponed. The ratio of the possible rate of water absorption to the rate of transpiration and growth becomes thus the real determining factor in the bog habitat and in the selection and in the distribution of plants. In all cases cultivated agricultural plants become flaccid and the roots appear gelatinous or as if burned black at the tips. The general dwarfing of roots (see illustrations in **7** and **8**) offers very little efficiency to physiologically arid conditions; nor is the change in form characters of shoot and leaf induced by the consequent lack of coordination of functions an advantage or an adaptation. Resistance to desiccation and the capacity for conserving water are more direct and more efficient responses to the limiting condition which the plants meet. This fact is not necessarily to be taken as valid in accounting for all highly specialized and inheritable structures so frequently met with in plants occurring in these habitats. The alteration of shoots and leaves in response to the stimulation of external factors may or may not increase fitness to the conditions, but it is safe to assume that the capacity for physiological changes and responses

controls the survival value of plant forms to a greater extent than has been admitted.

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BRIEFER ARTICLES

IS OPHIOGLOSSUM PALMATUM ANOMALOUS?

Under the unassuming title "Notes on the morphology of *Ophioglossum* (*Cheiroglossa*) *palmatum* L.," BOWER[1] has presented a paper containing generalizations of an unexpectedly far-reaching kind. Inasmuch as many of the arguments in this paper are directed against a paragraph in a recent paper by the present writer,[2] it seems desirable to make a few statements calculated to clear up the situation.

BOWER'S account is based on two fertile specimens obtained during a visit to Jamaica, also on a reexamination of herbarium specimens. He adheres to his previous view of the morphology of the plant,[3, 4] namely, that the several to many fertile spikes are derived by duplication or branching of the single spike found in *O. vulgatum*, in contrast to the usual view that the spikes represent fertile lobes of the leaf. Probably the most serious objection to the latter interpretation is the fact, brought out by BOWER, that some specimens show one or more of the *distal* spikes inserted on the adaxial face of the leaf in a more or less median position, while one might expect to find them inserted marginally. Unfortunately neither of the specimens from Jamaica, and in fact no specimen which has been available for sectioning, shows this critical feature. BOWER recognizes the importance of this method of study, for in a number of his figures he represents the vascular supply of fertile spikes. I wish to point out that each of the cases so represented (figs. 17, i–ix; 19, i–v; 20, i–vii) fits in with my interpretation of the fertile spike as either a single segment of the leaf or a fused pair of segments, so I must insist that until an opportunity occurs for demonstrating the origin of the vascular supply to the upper median spikes, my interpretation stands. At the same time, I cheerfully admit the possibility of BOWER'S view as an alternative theory, especially on the basis of the branching of fertile spikes, figured in 1896 for *O. pendulum* as well as *O. palmatum*. Is it

[1] Ann. Botany **25**: 277–298. *pls. 22–24*. 1911.

[2] The nature of the fertile spike in the Ophioglossaceae. Ann. Botany **24**: 1–18. *pls. 1, 2*. 1910.

[3] Studies in the morphology of spore-producing members. II. Ophioglossaceae. London. 1896.

[4] The origin of a land flora. London. 1908.

not possible, as has turned out in so many other cases, that the truth lies between the two extreme views? May it not be that the spikes of *O. palmatum* represent lobes of the leaf, and that certain of the upper ones in strong growing plants have suffered splitting or duplication? Such a view would take into account the effects of the peculiar life habits of this species, and at the same time would explain the identity in origin of the lower spikes with that found in the other members of the genus.

In his recent paper BOWER supports his interpretation by eight considerations, two of which are referred to above. Under one heading he urges the fact that "the identity of the margins of the leaf, so far as these are defined by the vascular strands, is entirely merged by the repeated fusions of the strands on the adaxial face of the elongated petiole" (p. 289). Yet, while describing the insertion of the petiolar strands on the central cylinder of the stem, BOWER shows that the leaf gap is obscured by a vascular commissure stretching across the gap at the point of attachment of the leaf trace bundles, and this fact does not cause a doubt as to the existence of a leaf gap. Apparently the anastomosing of vascular strands is characteristic of the plant, and the relationships of the parts can be best interpreted by comparison with simpler members of the family; this is what I have sought to do.

Professor BOWER'S caustic remarks concerning my paper on the Ophioglossaceae may the more readily be passed over in view of the fact that he has expressly repudiated his former view as to the relationships of the group, and hence accepts the main contention of my paper. With the candor characteristic of a true scientist, he has considered the evidence accumulated since 1896, and decides that the balance is in favor of allying the Ophioglossaceae with Filicales rather than with Lycopodiales. As a consequence of this, he regards the fertile spike not as a sporangiophore, but as one or more pinnae, here again agreeing with my conclusions. If now it is admitted that the fertile spike in most members of the group represents one pinna or a fused pair of pinnae, it is difficult for me to see why the interpretation should not be pushed to its logical end. The pinna nature of the fertile spike is most clearly seen in *Botrychium;* if the spike of *O. vulgatum* or *O. reticulatum* has a vascular supply which originates in a way similar to that of species of *Botrychium*, it may be regarded as representing two fused basal lobes of the leaf. The spike of *O. pendulum* has a similar vascular supply and may also be regarded as having the same morphological nature. A basal median spike in *O. palmatum* has a vascular supply identical with this; why then should it not be interpreted in the same way?

Marginal spikes situated above this would then represent single lobes of the leaf, comparable to the abnormal spikes of *B. obliquum* figured in my paper. In fact, the new figures representing sections through the base of fertile spikes more than ever convince me that there is an underlying unity in the family, in spite of the complications shown by *O. palmatum*. This unity appears in my interpretation of the fertile spike, and forms the only basis so far offered for comparison of all the members of the group.

Just what becomes of the order Ophioglossales remains slightly in doubt, for BOWER sometimes uses this term and sometimes the term Ophioglossaceae in his recent paper. Without entering into taxonomic considerations, it would appear that Ophioglossaceae might well remain a family of Filicales.

In conclusion it may be remarked that BOWER'S admirable summing up of the differences in the vascular supply of spore-producing organs among the Psilotaceae, Sphenophyllaceae, and Ophioglossaceae lends support to the view that the two great phyla Lycopsida and Pteropsida have been separated for a vast period of time.—M. A. CHRYSLER, *University of Maine, Orono, Me.*

CRYPTOMERIA JAPONICA

(WITH FOUR FIGURES)

At the Harvard Botanic Garden, there is a *Cryptomeria japonica* 8–10 feet high. When examined early this spring, many of the branches that bore female cones were seen to have produced abnormal growths. The central axis of the cone had in some cases elongated into a vegetative branch. This condition has often been noted before in *Pinus*, *Abies*, *Larix*, *Sciadopitys*, and some other conifers, as well as in *Cryptomeria*. The *Gardeners Chronicle*[5] in discussing proliferous cones says, "this condition is so common in our experience as to be nearly as frequently met with as the normal state." Then again in reference to *Cryptomeria*,[6] "a very common peculiarity is the proliferation of the axis beyond the cone in the form of a slender branchlet." This vegetative proliferation has also been described by PENZIG,[7] MASTERS,[8] EICHLER,[9] and others.

Another and apparently undescribed condition was observed in the

[5] Gard. Chron., January 28, 1882, p. 112.

[6] *Ibid.*, November 30, 1901, p. 389.

[7] Pflanzen Teratologie, Vol. II, p. 509.

[8] Vegetable teratology, p. 245.

[9] Excursions morphological, Nat. Hist. Rev., April 1864.

case of the tree at the Botanic Garden. It was found in certain instances that the proliferating axis, instead of being merely a leafy shoot, bore male cones. This condition, so far as the writer has been able to observe, has not hitherto been described. Owing to repairs being made at the greenhouses, this tree had been placed horizontally in a dark pit for the winter. This unnatural condition perhaps accounted for the abnormal growths.

FIGS. 1–4

Figs. 1 and 2 show female cones bearing clusters of male cones on their elongated axes. Fig. 3 shows a normal cluster of male cones and another cluster on the proliferated female cone. Fig. 4 shows a normal female cone on the left, a female cone on the right bearing a vegetative branch, and a female cone in the center bearing a cluster of male cones.—ANSEL F. HEMENWAY, *Harvard University*.

CURRENT LITERATURE

BOOK REVIEWS

Plant pathology

The growing interest in plant pathology is attested by the appearance recently of two new books and a journal dealing with this subject. Of the books, one, by STEVENS and HALL,[1] is the second to appear in the United States within a year. The other, also in English, is by MASSEE.[2] The new journal appears under the name *Phytopathology*, as the official organ of the American Phytopathological Society.

The book by STEVENS and HALL is written to meet the needs of those who are concerned with plant diseases from a practical standpoint, and who wish to identify diseases easily and quickly, and find definite directions for combatting them. In its general scheme it departs considerably from the usual treatment adopted in works on plant diseases. The method of treatment is such as seemed to the writers most serviceable for the end in view. The diseased plant is the important object under discussion. Technical details relating to structure and life histories of fungi are omitted. Characteristics of fungi are described only where the fungus itself is sufficiently conspicuous to form a distinguishing mark by which to recognize the disease, as in mildews. Otherwise reference to the causal organism is limited to the giving of its scientific name after the common name of each disease. This enables one to identify the disease described. In the same way life histories are discussed only in so far as is necessary for the understanding of certain diseases, as in the case of rusts, and then only in their general aspects. In general only such characteristics are mentioned as are obvious to the naked eye and will aid the practical man in identifying the diseases. This method of treatment has permitted an arrangement of the material in the body of the work based on the classification of host plants, instead of the usual arrangement according to the systematic sequence of the fungi.

The book begins with brief introductory sections on general subjects of practical importance, such as fungicides, spraying machinery, cost and profits of spraying, and similar topics. This part is of special value to the practical man, as it brings together information regarding the newer spraying mixtures and methods of combatting diseases which have been published in various papers not easily available. A short chapter on general diseases takes up

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[1] STEVENS, F. L., and HALL, J. G., Diseases of economic plants. 8vo. pp. x+513. *figs. 214.* New York: The Macmillan Co. 1910. $2.00.

[2] MASSEE, GEORGE, Diseases of cultivated plants and trees. 8vo. pp. xii+602. *figs. 171.* New York: The Macmillan Co. 1910. $2.25.

such diseases as "damping off," which are not restricted to particular species of plants. The rest of the book deals with "Special diseases of crops." The material is arranged according to the agricultural classification of plants, under such heads as pomaceous fruits, drupaceous fruits, small fruits, vegetable and field crops, cereals, fiber plants, trees and timber, and ornamental plants. The descriptions are clear and concise, giving such characteristics as enable the general reader to identify the disease. The book is illustrated by numerous halftones, which, however, are only of fair quality.

A feature peculiar to the book is the introduction of a unique popular nomenclature for the diseases described. This feature consists in the uniform construction of popular names, where none exist, by adding the ending -ose to the generic name of the organism causing the disease. Although this method of forming popular names has been used to some extent before by the authors and others, and consequently is not entirely an innovation here, it becomes conspicuous on account of the extent to which the idea is carried out. It is doubtful if such an arbitrarily constructed nomenclature can ever find wide acceptance, or if it is desirable; for popular names arise spontaneously, and have only local but forceful significance, which cannot be attained by names manufactured on a wholesale scale. In this case their acceptance would rather lead to a confusing monotony.

The book will be found extremely useful to those who have to do with the growing of plants. It will enable them readily to renew information on diseases known to them, and to identify new diseases not too obscure. Being alphabetically arranged, the book itself serves as a sort of host index, making the finding of material an easy matter. In each case is given what is known of methods of treatment, the matter of real importance to the grower.

The work of MASSEE is the outcome of the author's well-known *Text-book of plant diseases*, the last revised edition of which appeared in 1903. The growth of plant pathology in the interval has made necessary a complete revision of the text, with the addition of so much new material that the result is a new book. While it follows the general plan of the older work, the treatment of the subject is much more extended, owing partly to the enlarged scope of the new book, but more directly to the amount of new material incorporated and to the fuller treatment accorded to the individual subjects.

The book begins with introductory sections discussing such general subjects as primary and secondary causes of disease, epidemics, infection of plants, the dissemination of fungous diseases, injuries not due to fungi, and other related subjects. Space is also given to the discussion of fungicides and spraying. The American reader will be struck by the absence from this section of a discussion of apparatus for the application of fungicides.

The greater part of the book is taken up with descriptions of diseases and the fungi causing them. This part is arranged according to the groups of fungi, although none of the ordinary systems of classification are followed in detail. In the Pyrenomycetes, for example, the spore characters are taken

as the primary basis for the arrangement, thus leading to an association of genera entirely different from that usually found in taxonomic works. By this method of classification, the genera of the Hypocreales and Dothidiales are distributed among the Sphaeriales. In the descriptions both the characteristics of the diseases and the life histories and characteristics of the causal organisms are given. The scheme is similar to that followed in the author's *Text-book*, but the accounts are much more complete as to detail than those of the former work. In the last part of the book some of the diseases and injuries caused by animals are described. Notes on several diseases which could not be incorporated in the body of the work are appended in the addendum. The book is illustrated by halftones of drawings.

The work forms a useful handbook of general information on plant diseases. The older and better known facts receive full and careful treatment, but with regard to the newer facts of plant pathology, the work shows a lack of critical consideration of the literature which greatly impairs its value as a reliable reference book. A few instances illustrating this point may be cited. The rotting of lettuce in greenhouses is still attributed to *Botrytis cinerea* (*Sclerotinia Fuckeliana*) (p. 263), although the investigations of SMITH[3] several years ago have shown that *Sclerotinia Libertiana* is the principal cause of this rot, while *Botrytis*-forms are only of secondary importance. These two fungi, although related, differ greatly in their mode of life, *Botrytis* being a common saprophyte everywhere, while *S. Libertiana* is a soil fungus. This great difference in the mode of life of the two fungi is of importance when methods of combatting them are considered. The wilt disease of cotton and other plants is described (p. 228) under *Neocosmospora* (misspelled *Neocosmopara* in the page-heading, subject-heading, and text, and still different in the index). A symptom of the same disease is described (p. 494) under its old name "Cotton Frenching," caused by *Fusarium vasinfectum*. The genetic relationship between these two fungi has been shown by SMITH.[4] Spraying for peach leaf curl is regarded as of little value because the perennial mycelium of *Exoascus deformans* in the shoots produces a crop of diseased leaves each year in spite of spraying. As a matter of fact, there is no disease that can be controlled with more certainty and with more striking results by spraying than the peach leaf curl. Furthermore, the careful investigations of PIERCE[5] have shown that the origin of the spring infection is still obscure, but that probably the perennial mycelium in the branches has very little to do with the early infection. The common apple blotch fungus the author suggests

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[3] SMITH, RALPH E., *Botrytis* and *Sclerotinia;* their relation to certain plant diseases and to each other. BOT. GAZETTE **29**:369–407. *pls. 3. figs. 3.* 1900.

[4] SMITH, ERWIN F., Wilt disease of cotton, watermelon, and cowpea. U.S. Dept. Agric., Div. Veg. Physiol. and Path., Bull. 17. 1899.

[5] PIERCE, NEWTON B., Peach leaf curl; its nature and treatment. U.S. Dept. Agric., Div. Veg. Physiol. and Path., Bull. 20. 1900.

(p. 412) is a stage of the apple scab fungus, yet these fungi could scarcely be confounded by one who had seen them. Under the heading "Peach leaf blotch (*Gloeosporium cydoniae* Mont.)," this disease is said to cause spots on the "living leaves of the peach (*Cydonia vulgaris*)." *Sphaeropsis malorum* is described only as a leaf spot disease of the apple, although it has been longest and best known as the cause of the black rot of the fruit, and later as the cause of a serious bark canker of apple trees.

The new journal *Phytopathology* is to be issued for the present as a bi-monthly publication of the American Phytopathological Society. The aim, as set forth in the editorial announcement, is "to provide a place for the publication of phytopathological papers which would otherwise be lost or scattered in various places." While much of its space will be occupied by papers read before the society, it is the policy of the editors to make the journal more broadly representative and to open its pages to contributions of value from any source. It is of octavo size, containing at present about 35 pages of text and a number of plates in each issue. The halftone plates are of unusually good quality. The first issue is fittingly introduced by an excellent halftone portrait of DEBARY, with a brief sketch of his life and of the influence of his great personality on the advancement of plant pathology.

Heretofore the chief interest in plant pathology in the United States has been on its economic side, and this side has been highly developed as a result of the facilities for investigation, and for the ready means for publication of results having an economic bearing, offered by the experiment stations. As a result of the emphasis on the economic point of view, little attention has been given to the more fundamental problems relating to the subject. Such phases as the physiological relations between the host and parasite, the changes in metabolism brought about by the parasites, and the enzymatic activities of parasites, have remained almost uninvestigated. A journal like the present one, devoted entirely to the interests of plant pathology and not restricted to the purely economic phases of the subject, will undoubtedly do much to stimulate research in these deeper problems of plant pathology.—H. HASSELBRING.

Fossil plants

The second volume of SEWARD'S *Fossil plants*[6] has remained too long unnoticed by this journal. The first volume appeared in 1898, and the general purpose and method of the work were stated in the review published at that time.[7] The thirteen years that have elapsed have been memorable ones in the history of paleobotany, so that if this second volume had appeared as

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[6] SEWARD, A. C., Fossil plants; a text-book for students of botany and geology. Vol. II. pp. xxii+624. *figs. 265*. Cambridge: The University Press; New York: G. P. Putnam's Sons. 1910. $5.00.

[7] Rev. in BOT. GAZETTE **26**:59. 1898.

promptly as at first expected, it would have been sadly out of date by this time. So large an addition has been made to our knowledge of fossil plants, that now we are to have three volumes of this work, instead of two, and the third volume, promised to appear "with as little delay as possible," is to contain the seed plants, and also a much-needed discussion of the geographical distribution of plants at different stages in the history of the earth.

The present volume contains the pteridophytes, with the exception of Equisetales and the major part of Sphenophyllales, which were treated in the first volume. As has been said often in this journal, the material of paleobotany must be traversed critically by morphologically trained paleobotanists, so that morphologists may be able to base their conclusions upon reasonably assured data. Even yet, most paleobotanists are stratigraphers, their chief concern being to be able to recognize a given horizon by a given form, whatever its relationships may be. Of course, such paleobotanists are geologists rather than botanists.

SEWARD has now done this service for botanists in the very critical series of fossil pteridophytes, and we are able to put together two or three competent and independent judgments, feeling well assured if we find agreement, and feeling cautious if we find disagreement. It is impossible to discuss the details of such a book, for it is more a manual than a reading text. It will be sufficient to indicate the titles of the 16 chapters.

XII, Sphenophyllales (continued) (16 pp.); XIII, Psilotales (13 pp.); XIV, Lycopodiales (62 pp.); XV, Arborescent Lycopodiales (104 pp.); XVI, Sigillaria (31 pp.); XVII, Stigmaria (21 pp.); XVIII, Bothrodendreae (23 pp.); XIX, Seed-bearing plants closely allied to members of the Lycopodiales (9 pp.); XX, Filicales (44 pp.); XXI, Fossil ferns (71 pp.); XXII, Marattiales (fossil) (17 pp.); XXIII, Psaronieae (15 pp.); XXIV, Ophioglossales (fossil) (5 pp.); XXV, Coenopterideae (91 pp.); XXVI, Hydropterideae and Sagenopteris (11 pp.); XXVII, Genera of Pteridosperms, ferns, and *plantae incertae sedis* (97 pp.).

These titles do not indicate any coordination, but perhaps they represent the legitimate state of mind in the presence of the material.—J. M. C.

MINOR NOTICES

New Zealand plants.—New Zealand is fortunate in having as its leading botanist one who has not only carefully studied the problems of plant life in a comparatively new region, but has now given to the general public a most interesting volume[8] on the vegetation of these islands. Beginning with a simple synopsis of the history of botanical explorations in New Zealand, from the work of Dr. JOHN FORSTER in 1773 to the present day, Dr. COCKAYNE proceeds to discuss the most notable features of a vegetation ranging from a

[8] COCKAYNE, L., New Zealand plants and their story. 8vo. vii+190. *figs.* 71. 1910. Wellington: John Mackay, Government Printer.

rain forest of almost tropical luxuriance to xerophytic sand dunes. The ecological viewpoint is maintained throughout, although the fact that the author is writing for a general audience seems to have led him from his usual scientific accuracy to many teleological interpretations. Still, the story of the New Zealand plants is told in so clear and interesting a manner that many botanists of other lands will find the little volume useful in imparting a picture of the vegetation of that distant country. For local use it cannot but be of the greatest service to teachers who are seeking an intelligent appreciation of their surroundings. The needs of the teaching profession are further recognized by a chapter on the cultivation of indigenous plants on the school grounds and in the school garden. The botanist will be interested, among other things, in the considerable number of plants with juvenile and adult leaf forms. The value of the volume is much increased by 70 illustrations from photographs of some of the most remarkable plants described.—GEO. D. FULLER.

North American Flora.[9]—Volume XXV, part 3, continues the treatment of the Geraniales and includes an elaboration of the Rutaceae and Surianaceae by PERCY WILSON, the Simaroubaceae by JOHN KUNKEL SMALL, and the Burseraceae by JOSEPH NELSON ROSE. New species, chiefly from Cuba and Mexico, are described in the following genera: *Ravenia* (1), *Zanthoxylum* (3), *Spathelia* (1), *Amyris* (1), *Elaphrium* (7), and *Icica* (10). One new genus (*Castelaria*) of the *Simaroubaceae* is proposed, based on *Castela Nicholsoni* Hook., to which are referred 8 species, 2 from Cuba being new to science.—J. M. GREENMAN.

Symbolae Antillanae.[10]—The publication of a third fascicle completes the sixth volume of Professor URBAN'S well-known work, *Symbolae Antillanae.* The fascicle recently issued continues the treatment of the Orchidaceae by A. COGNIAUX. There are recognized 96 genera, to which are referred 505 species, 28 being new to science. The excellent keys, careful and full descriptions, copious citation of exsiccatae, and complete synonomy with bibliography, make this a thoroughly scientific and standard work on the Orchidaceae of the Antillean region.—J. M. GREENMAN.

Handbook of deciduous trees.—The tenth part (fifth section of second volume) of SCHNEIDER'S *Handbuch* has just appeared,[11] the preceding part

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[9] North American Flora, Vol. XXV, part 3, pp. 173–261. New York Botanical Garden. May 6, 1911.

[10] URBAN, I., Symbolae Antillanae seu fundamenta florae Indiae Occidentalis. Vol. VI, fasc., 3., pp. 433–721. Leipzig: Fratres Borntraeger. 1910.

[11] SCHNEIDER, C. K., Illustriertes Handbuch der Laubholzkunde. Zehnte Lieferung (fünfte Lieferung des zweiten Bandes). Imp. 8vo. pp. 497–757. *figs. 329–419.* Jena: Gustav Fischer. 1911. *M* 5.

having appeared in 1909.[12] It contains descriptions, with illustrations, of the angiospermous trees of central Europe, both native and under cultivation. The present part begins in the midst of *Rhododendron* and ends with *Viburnum*. —J. M. C.

NOTES FOR STUDENTS

Current taxonomic literature.—E. BRAINERD (Bull. Torr. Bot. Club **38**: 1–9. *pl. 1.* 1911) presents an article entitled "Further notes on the stemless violets of the South," and describes two new varieties.—R. E. BUCHANAN (Mycologia **3**:1–3. *pls. 34, 35.* 1911) describes and illustrates a new hyphomycete (*Thyrococcum humicola*), obtained from pure cultures.—C. DE CANDOLLE (Phil. Journ. Sci. Bot. **5**:405–463. 1910) presents "A revision of Philippine Piperaceae" in which he recognizes 22 species of *Peperomia* and 123 of *Piper*. Of the total number about 50 are new to science.—J. CARDOT (Rev. Bryol. **38**:33–43. 1911) under the title "Diagnoses préliminaires de Mousses mexicaines" has published several new species of mosses, based mainly on collections made in southern Mexico by C. R. BARNES and W. J. G. LAND in 1908.—C. CHRISTENSEN (Arkiv för Bot. **10**[2]:1–32. *pl. 1.* 1910) presents an article "On some species of ferns collected by Dr. CARL SKOTTSBERG in temperate South America" in 1907–1909. The paper includes descriptions of 3 species new to science.—W. N. CLUTE (Fern Bull. **18**:97, 98. 1910) describes and illustrates a new species of *Polypodium* (*P. prolongilobum*) and a new variety of *P. vulgare* L. from Arizona.—E. B. COPELAND (Leafl. Phil. Bot. **3**:791–851. 1910) enumerates upward of 250 species of ferns from Mount Apo, Philippine Islands; of this number 16 are described as new. The author states: "It is probable that this is the richest known fern flora in the world." *Polypodium* and *Dryopteris* are the predominating genera.—A. D. E. ELMER (Leafl. Phil. Bot. **3**:853–1107. 1910–1911) records further data concerning the flora of the Philippine Islands, and describes 138 species of flowering plants as new.—M. L. FERNALD (Rhodora **13**:4–8. 1911)has published a new species of *Scirpus* (*S. Longii*) from Massachusetts and New Jersey.—D. GRIFFITHS (Rep. Mo. Bot. Gard. **21**:165–175. *pls. 19–28.* 1910) in continuation of his studies on the genus *Opuntia* has described and illustrated 10 new species indigenous to southwestern United States and northern Mexico.—E. HASSLER (Rep. Nov. Sp. **9**:1–18, 49–63, 115–121. 1910–1911) has published several new species, varieties, and forms in the genus *Mimosa* and in the families Bignoniaceae and Solanaceae from Paraguay. One new genus (*Rojasiophyton*) of the Bignoniaceae is proposed.—F. D. HEALD and F. A. WOLF (Mycologia **3**:5–22. 1911) have published 41 new species of Texan fungi.—A. A. HELLER (Muhlenbergia **7**:1–11, 13–15. 1911) records further results of his studies on "The North American lupines" and describes two new species: *L. sabulosus* from the sand hills near San Francisco and *L. apodotropis* from Oregon.—A. F. G. KERR and W. G. CRAIB (Kew Bull. 1–60. 1911) under the general title of

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[12] BOT. GAZETTE **48**:312. 1909.

"Contributions to the flora of Siam" have issued an interesting paper on the little known flora of that region. A general sketch of the vegetation is from the pen of Dr. KERR, and a "List of Siamese plants with descriptions of new species" is the work of Mr. CRAIB. Several new species are added to the flora and one new genus (*Pittosporopsis*) of the Icacinaceae is proposed.—W. LIPSKY (Acta Hort. Petrop. **26**:119–616. *pls. 3–6.* 1910) continues his important publications on the flora of central Asia. The present contribution contains descriptions of several new species, particularly in *Astragalus* and *Potentilla*. The treatment of the latter genus was contributed by the noted specialist TH. WOLF.—T. H. MACBRIDE (Mycologia **3**:39, 40. *pl. 36.* 1911) describes and illustrates a new genus (*Schenella*) doubtfully referred to the Myxomycetes. The material on which the genus is based was found growing on a decaying pine log in the Yosemite Valley, California.—M. E. MCFADDEN (Univ. Calif. Pub. Botany **4**:143–150. *pl. 19.* 1911) presents an account of "A Colacodasya from southern California," and in conjunction with Dr. W. A. SETCHELL describes a new species (*C. verrucaeformis*) found growing on *Mychodea episcopalis* J. Ag.—E. D. MERRILL and M. L. MERRITT (Phil. Journ. Sci. Bot. **5**:371–403. *pls. 1–4. 1 map.* 1910) in a concluding article on "The flora of Mount Pulog" have published 11 new species of Sympetalae. Two new genera are described by Mr. MERRILL, namely *Loheria* of the Myrsinaceae and *Merrittia* of the Compositae.—W. A. MURRILL (Mycologia **3**:23–36, 79–91. 1911) has issued the first two papers of a proposed series of articles on "The Agaricaceae of tropical North America," recording new species in *Leucomyces*, *Limacella*, *Russula*, *Lentinus*, and *Lepiota*.—G. E. OSTERHOUT (Muhlenbergia **7**:11, 12. 1911) describes a new species of *Schmaltzia* (*S. pubescens*) and one of *Carduus* (*C. vernalis*) from Colorado.—F. W. PENNELL (Torreya **11**:15, 16. 1911) records a new species of *Gerardia* (*G. racemulosa*) from New Jersey.—C. B. ROBINSON (Phil. Journ. Sci. Bot. **5**:465–543. 1910) begins a monographic consideration of the "Philippine Urticaceae," treating 9 genera to which are referred 86 indigenous species, about one-half being new to science. One new genus (*Elatostematoides*) is proposed.—E. ROSENSTOCK (Rep. Nov. Sp. **9**:67–76. 1910) has published 16 new species of ferns, 5 of which are from Costa Rica.—P. A. RYDBERG (Bull. Torr. Bot. Club **38**:11–23. 1911) in continuation of his "Studies on the Rocky Mountain flora" has described several new species of Compositae.—G. SCHELLENBERG (Mitt. Bot. Mus. Univ. Zürich, No. 50, pp. 1–158. 1910) under the title "Beiträge zur vergleichenden Anatomie und zur Systematik der Connaraceen" has published the results of a detailed study of this family, recognizing 17 genera and over 100 species. One new genus (*Santaloides*), based on *Rourea Afzelii* Planch. from Africa, is new to science.—A. K. SCHINDLER (Rep. Nov. Sp. **9**:123–125. 1911) under the title "Halorrhagaceae novae I" includes two new species of *Gunnera* from Peru.—R. SCHLECHTER (*ibid.* 21–32) has published 20 new species of orchids, 13 of which are from Central and South America.—F. J. SEAVER (Mycologia **3**:57–66. 1911) publishes the results of studies in Colorado fungi and includes descriptions of

two new species, namely *Ascobolus xylophilus* and *Godronia Betheli*.—D. R. SUMSTINE (*ibid.* 45–56. *pls. 37–39*) under the title "Studies in North American Hyphomycetes I" presents a taxonomic treatment of *Rhinotrichum* and *Oliptrichum*, recognizing for the former 13 species, of which 3 are new to science.—F. THEISSEN (Broteria, Ser. Bot. **9**:121–147. *pls. 5–9*. 1910) in an article entitled "Hypocreaceae Riograndensis" has published 15 new species. The same author (Beih. Bot. Centralbl. **27**^{2}:384–411. 1910) under the title "Fungi Riograndensis" lists about 150 species from southern Brazil, 10 of which are new to science. One new genus (*Creosphaeria*) is characterized and is said to be intermediate between *Rosellinia* and *Hypoxylon*.—I. TIDESTROM (Am. Mid. Nat. **1**:165–171. *pl. 11*. 1910) has published 3 new species of *Aquilegia* from western United States and gives a synopsis of 10 recognized species.—I. URBAN (Ber. Deutsch. Bot. Gesell. **28**:515–523. *pl. 15*. 1911) has published a new species of *Loasa* (*L. Plumeri*) and a new monotypic genus (*Fuertesia*) of the Loasaceae from Sto. Domingo.—W. WEINGART (Monats. für Kakteenkunde **21**:5–7. 1911) describes a new species of *Phyllocactus* (*P. Eichlamii*) from Guatemala.—R. S. WILLIAMS (Bull. N.Y. Bot. Gard. **6**:227–261. 1910) under the title "Bolivian Mosses, Part II," has described 18 new species. The same author (Bull. Torr. Bot. Club **38**:33–36. 1911) records two new species of mosses from Panama.—N. N. WORONICHIN (Bull. Jard. Imp. Bot. St. Petersb. **11**:8–19. 1911) records a list of fungi collected in southeastern Russia, and includes a new ascomycetous genus (*Rhodosticta*) parasitic on the leaves of *Caragana frutex* Koch.—J. M. GREENMAN.

The number of chromosomes.—In 1909 STRASBURGER made a cytological study of the parthenogenetic *Wikstroemia indica*, and now he has succeeded in securing from the rather inaccessible Himalaya region material of the nearly related *W. canescens*, in which fertilization regularly occurs. From an investigation of *W. canescens* and a study of the literature of forms with unexpectedly large numbers of chromosomes, some interesting conclusions are reached.[13]

High chromosome numbers can be shown to be the result of multiplication of whole chromosomes, so that the organism becomes polyploid, with a diploid gametophyte and tetraploid sporophyte, instead of the usual haploid and diploid generations. Such increases in chromosome numbers must be referred to mitotic division, which does not get to the separation of the daughter chromosomes, or, if daughter nuclei are formed, they reunite. The increase in number comes usually from a longitudinal division, which gives like products, and it is probable that the phenomenon takes place in the fertilized but not yet divided egg. The increase in the number of chromosomes is accompanied by some increase in the size of the nucleus and protoplast.

In the nuclei of sporophytes which are more than diploid, the homologous

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[13] STRASBURGER, EDUARD, Chromosomenzahl. Flora **100**:1–50. *pl. 6*. 1910.

chromosomes are grouped in pairs, and not in tetrads in tetraploid nuclei. In the triploid nuclei of the endosperm of angiosperms, there are both paired and unpaired chromosomes. In the mother cells of polyploid plants there are always only bivalent chromosomes (gemini), and never a complex of more than two chromosomes as elements of the reduction plate. In triploid nuclei of the sporophyte of hybrids which result from a union of haploid and diploid gametes, there are both paired and single chromosomes, and in the mother cells of such plants both paired and single chromosomes appear. From a study of the various pairings it seems that they depend upon an attraction between homologous chromosomes, so that this homology, rather than any maternal or paternal origin, determines the formation of pairs, and it may be possible that a pair of two homologous chromosomes may be derived from the same sex product. The increase in the number of chromosomes has often led to parthenogenesis (*eiapogamy*), but there is also parthenogensis without any increase in the number of chromosomes.

The large number of chromosomes does not always result from longitudinal division, but may be due to a transverse division, and in this case there is no increase in the size of the nucleus and no loss of sex occurs. Zoological literature shows many instances of analogous phenomena.

This paper suggests a wide range of problems for cytological investigation, and obviously it has an important bearing upon the theory of the individuality of the chromosome.—CHARLES J. CHAMBERLAIN.

Sixteen-nucleate embryo sacs.—The ovule of *Euphorbia procera*[14] has several hypodermal archesporial cells, each of which divides into a tapetal cell and a megaspore mother cell. The two reduction divisions take place in the mother cells, but are not accompanied by wall formation, so that each megaspore mother cell now contains four megaspore nuclei, or rather, four megaspores not separated by walls. At this stage all the tetrads degenerate except one, and in this each megaspore nucleus undergoes two successive mitoses, giving rise to a 16-nucleate sac. Several other species of *Euphorbia* were examined, and all had a single archesporial cell and a typical 8-nucleate sac.

MODILEWSKI[15] had previously shown that in the 16-nucleate stage of *E. procera* the nuclei are arranged in four tetrad-like groups, from each of which one nucleus moved to the center of the sac to form the endosperm nucleus. The micropylar group formed the egg apparatus and the chalazal group the antipodals, while the two lateral groups resembled the egg apparatus. Double fertilization was observed, the second male nucleus fusing with the four nuclei at the center of the sac, so that the endosperm nucleus resulted from the fusion of five nuclei. The chromosome situation was not determined.

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[14] MODILEWSKI, J., Weitere Beiträge zur Embryobildung einiger Euphorbiaceae. Ber. Deutsch. Bot. Gesell. **28**:413–418. *pl. 12.* 1910.

[15] ———, Zur Embryobildung von *Euphorbia procera*. Ber. Deutsch. Bot Gesell. **27**:21–26. *pl. 1.* 1908.

MODILEWSKI[16] has also described a 16-nucleate embryo sac in *Gunnera chilensis*, in which case the four megaspores, not separated by walls, all take part in forming the embryo sac. Although no definite proof was obtained, he believed the embryos to be parthenogenetic.

An interesting embryo sac is described by DESSIATOFF,[17] who finds 16 nuclei in *Euphorbia virgata* at the fertilization period. The 16 nuclei come from one megaspore, and consequently the situation is somewhat different from that found in *Peperomia*, where 4 megaspores enter into the formation of the sac. The 16 nuclei are arranged in four groups of four each, and one nucleus from each group moves to the center of the sac, where the four fuse to form the endosperm nucleus. There are three antipodals, and an egg apparatus of two synergids, and an egg. The two other groups remain at the side of the sac and resemble the egg apparatus. In general, this embryo sac resembles that of the Penaeaceae as described by Miss STEPHENS.—CHARLES J. CHAMBERLAIN.

The sperm nuclei of Lilium.—Since zoological literature furnishes no instance of the fertilization of the egg by a naked male nucleus unaccompanied by any cytoplasm, and since the male nucleus in plants has in nearly all cases been shown to be accompanied by cytoplasm, definite proof of fertilization by a naked nucleus is worth recording, especially since the nucleus is regarded by many as the sole bearer of hereditary qualities. Both STRASBURGER and KOERNICKE have claimed that in *Lilium* the sperm nucleus, at the time of fertilization, is not accompanied by any cytoplasm. A paper by NAWASCHIN,[18] the discoverer of double fertilization, gives a very complete account of the generative cell and development of the sperm nuclei in the classic *Lilium Martagon*. The excellent technic, remarkably close series of stages, and the carefully drawn illustrations, all support NAWASCHIN'S description and conclusions. The cytoplasm of the generative cell has a finely granular structure up to the anaphase of the division of its nucleus, at which time its cytoplasm begins to mingle with the general cytoplasm of the pollen tube. The mitosis which gives rise to the two male nuclei is characterized at every stage by sharply differentiated chromosomes, so that the sperm nuclei do not reach the resting stage, but remain in the condition characteristic of telophase. Consequently, it is not improbable that the mature nuclei are capable of movement. The achromatic spindle is scanty and in some cases doubtful, and in others cannot be identified at all, so that it is probable that

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[16] MODILEWSKI, J., Zur Embryobildung von *Gunnera chilensis*. Ber. Deutsch. Bot. Gesell. **26a**:550–556. *pl. 11*. 1908.

[17] DESSIATOFF, N., Zur Entwickelung des Embryosackes von *Euphorbia virgata*. Ber. Deutsch. Bot. Gesell. **29**:33–39. *figs. 17*. 1911.

[18] NAWASCHIN, SERGIUS, Näheres über die Bildung der Spermakerne bei *Lilium Martagon*. Ann. Jard. Bot. Buitenzorg. II. Supplement III. 871–904. *pls. 33, 34*. 1910.

the chromosomes in this mitosis move independently of any spindle.—C. J. CHAMBERLAIN.

Studies in ferns.—Apogamy in *Cystopteris fragilis*, hybridization in *Asplenium*, and conditions of heredity in certain ferns, have been investigated by A. HEILBRONN.[19] The group last considered includes, as true varieties, the following: *Aspidium Filix-mas* var. *grandiceps*, *A. aculeatum* var. *cruciato-polydactylum*, *Athyrium Filix-femina* var. *corymbiferum*, *A. Filix-femina* var. *multifidum*, *A. Filix-femina* f. *multifidum Mapple-Beckii*, *A. Filix-femina* var. *laciniatum* and var. *purpureum* Lowe. Others not considered true varieties are *Athyrium Filix-femina* var. *Fieldiae* Moore, *A. Filix-femina* f. *multifidum minus*, and *Aspidium angulare* f. *grandidens*. The general conclusions of the author are: (1) *Cystopteris fragilis* f. *polyapogama* develops prothallia which show the power of developing sporophytes from unfertilized egg cells or by vegetative apogamy, the two cases sometimes being side by side; (2) the question as to whether *Asplenium germanicum* is a hybrid between two forms is not yet settled, but by crossing *Asplenium septentrionale* (female) and *A. Ruta-muraria* (male), a plant was obtained which stands nearer to *A. germanicum* than any other known form; (3) some fern-forms which had not been investigated before appear apogamous. Of the different forms of *Athyrium Filix-femina* from England, some are true varieties and some revert. Attempts to obtain forkings artificially were unsuccessful.—NORMA E. PFEIFFER.

Water-cultures of fern prothallia.—In a short paper H. FISCHER[20] gives some of his results with the germination of fern spores, in obtaining material for his work on variation, hybridization, etc. He states the advantages of water-cultures over solid substrata as being threefold: the chemical constitution can be regulated; the cultures are cleaner, and material is fit for microtome sections without extra care; the spores may be sowed as thick as desirable, and easily diluted, like a solution, if too close together on germination. The danger lies in the drying out of cultures, or too great evaporation, resulting in plasmolysis. A second danger lies in the production of abnormal forms by too deep layers. The author recommends Pfeffer's nutrient solution and Arthur Meyer's solution, the formula of which he gives. He finds that changing one compound or its concentration, changing the reaction of a solution, etc., often produce the desired germination. But evidently there is no general rule for this, as there is none for the length of time after ripening that a spore will germinate. In *Asplenium Serra*, herbarium material germinated after 48 years. In some few cases the author is as yet unable to induce germination.—NORMA E. PFEIFFER.

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[19] HEILBRONN, ALFRED, Apogamie, Bastardierung, und Erblichkeitsverhältnisse bei einigen Farnen. Flora (n.s.) **1**: 1–42. *figs. 43*. 1910.

[20] FISCHER, HUGO, Wasserkulturen von Farnprothallien, mit Bemerkungen über die Bedingungen der Sporenkeimung. Beih. Bot. Centralbl. **27**[1]: 54–59. 1911.

Development of banana pollen.—An extensive investigation[21] of three races of the edible banana (*Musa sapientum*) has shown that they can be distinguished by the number of chromosomes, "*Dole*" having 8, "Radjah Siam" 16, and "Kladi" 24, as the haploid numbers, so that the races might be designated as vars. *univalens*, *bivalens*, and *trivalens*. The volume of the nuclei, but not their surfaces, is in the ratio 1:2:3. With the increase in the number of chromosomes came disturbances in the development of pollen, some of the chromosomes not passing to the poles, but remaining behind and forming extra nuclei. The size of the tetrad varies in a given anther, although the number of chromosomes in the entire tetrad is constant. Sometimes as many as eight pollen grains are formed from a single mother cell.

Prochromosomes are easily distinguished in the pollen mother cell, and in *Musa Dole* TISCHLER was able to show that the number of prochromosomes was equal to the diploid number of chromosomes. Probably there is a fusion of prochromosomes at synapsis. The splitting of chromosomes at the strepsonema stage TISCHLER regards as genuine and not merely apparent.—CHARLES J. CHAMBERLAIN.

Parthenogenesis in Taraxacum.—Parthenogenesis in *Taraxacum* has been investigated again, this time by SCHKORBATOW[22] who writes in Russian, but adds a summary in German, from which the following points are taken: The removal of anthers does not in any way affect the germination of seeds. Various colors of seeds, like clear green and dark brown, may become fixed and hereditary. At metaphase of the first division in the embryo sac, the chromosomes show various and characteristic forms, but the chromosomes seldom take the arrangement belonging to the heterotypic mitosis, and when they do, the author regards the phenomena as atavistic. Amitotic divisions occur in the embryo sac, in the endosperm, and in early stages of the embryo, in the last case all the nuclei but one becoming resorbed, so that the cells are left uninucleate.—CHARLES J. CHAMBERLAIN.

The origin of the vacuole.—Probably most botanists believe that the large vacuoles of plants arise by the coalescence of numerous smaller ones. A paper by BENSLEY,[23] dealing with the canalicular apparatus of animals, gives also a description of root tips and the tapetum of anthers. The fixing agent used was: neutral formalin (freshly distilled), 10 cc.; water, 90 cc.; potassium bichromate, 2.5 g.; mercuric chloride, 5.0 g. With this fixing

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[21] TISCHLER, G., Untersuchungen über die Entwickelung des Bananen-Pollens. I. Archiv. für Zellforschung **5**:622–670. *pls. 30, 31.* 1910.

[22] SCHKORBATOW, L., Parthenogenetische und apogame Entwickelung bei den Blüthenpflanzen. Entwickelungsgeschichtliche Studien an *Taraxacum officinale* Wigg. Bot. Institut Charkow. pp. 43. *pl. 1. figs. 4.* 1910.

[23] BENSLEY, R. R., On the nature of the canalicular apparatus of animal cells. Biol. Bull. **19**:174–194. *figs. 1–3.* 1910.

agent and Haidenhain's iron alum haematoxylin, or Flemming's triple stain, the young cells, especially of the dermatogen and plerome, show an intricate network of canals, and older cells show a gradual transition from the network, which is a single structure, to the familiar appearance obtained by current methods. This method promises to solve the problem of the origin of the vacuole, and at the same time it is excellent for nuclear structures.—CHARLES J. CHAMBERLAIN.

Mitochondria.—The small bodies variously known as mitochondria, chondriosomes, chondriokonten, and chromidial substance, have been known to zoologists for some time, but it is only recently that they have attracted any serious attention among botanists. A short paper by LEWITSKI[24] describes the mitochondria in young cells of *Pisum sativum* and *Asparagus officinale*. In the root tip the mitochondria become transformed into leucoplasts, and in the stem tip into chloroplasts. The mitochondria divide and are believed to be an essential part of the cytoplasm. No mitochondria were found inside the nucleus, and the author does not believe that there is any passage of mitochondria between nucleus and cytoplasm. Division of mitochondria is figured and described.—CHARLES J. CHAMBERLAIN.

Origin of the plastid.—For nearly twenty years the theory that the plastid is a permanent organ of the cell, arising only by the division of a preexisting plastid, has been generally accepted, doubtless on account of the thorough investigations of SCHIMPER and of MEYER. When LEWITSKI's paper appeared, claiming that plastids arise from chondriosomes, MEYER[25] at once denied the claim and demanded proof. For several years the reviewer has doubted the accuracy of the conclusion reached by both SCHIMPER and MEYER that the plastid arises only by the division of a pre-existing plastid. Their evidence seems more voluminous than convincing. It is to be hoped that this incipient controversy will settle the status of the plastid.—CHARLES J. CHAMBERLAIN.

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[24] LEWITSKI, G., Ueber die Chondriosomen in pflanzlichen Zellen. Ber. Deutsch. Bot. Gesell. **28**:538–546. *pl. 17*. 1910.

[25] MEYER, ARTHUR, Bermerkungen zu G. LEWITSKI: Ueber die Chondriosomen in pflanzlicher Zellen. Ber. Deutsch. Bot. Gesell. **29**:158–160. 1911.

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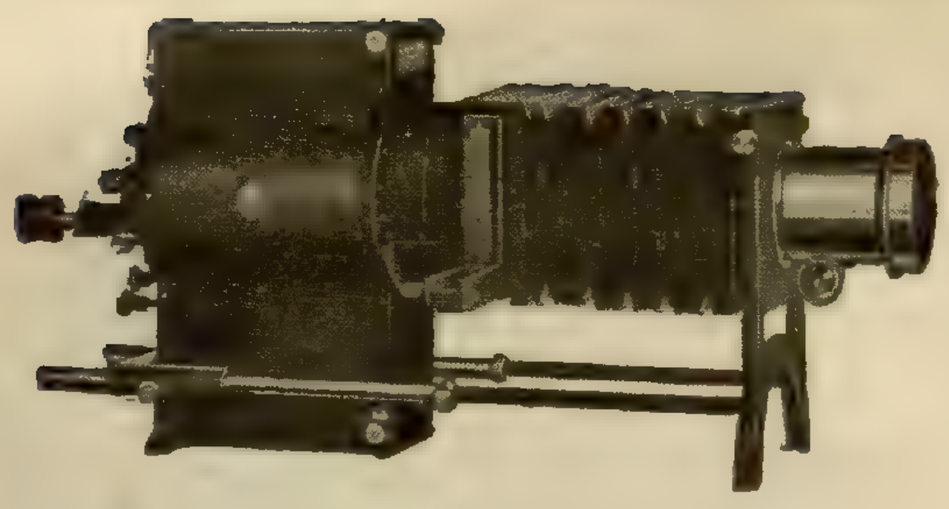

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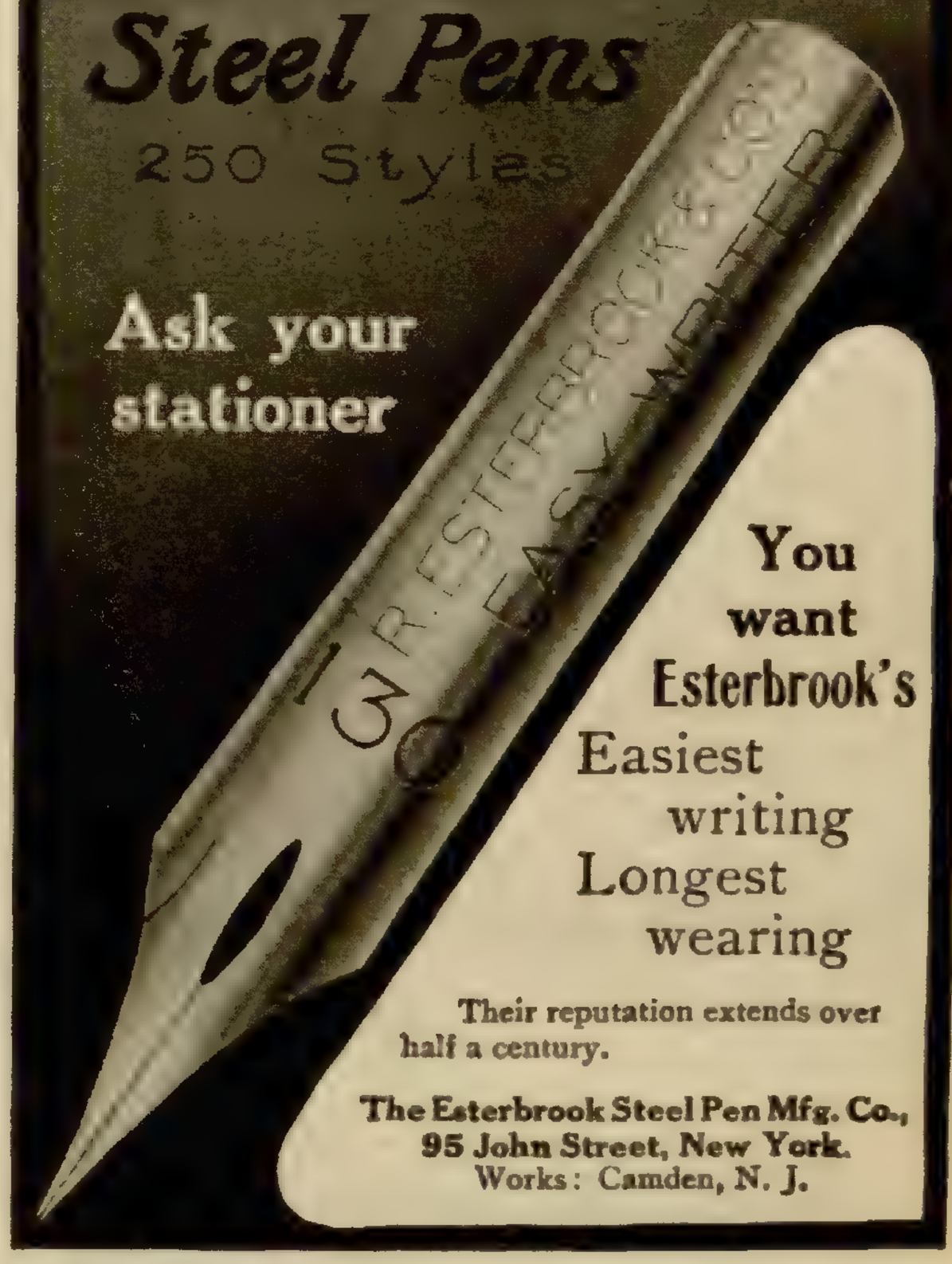

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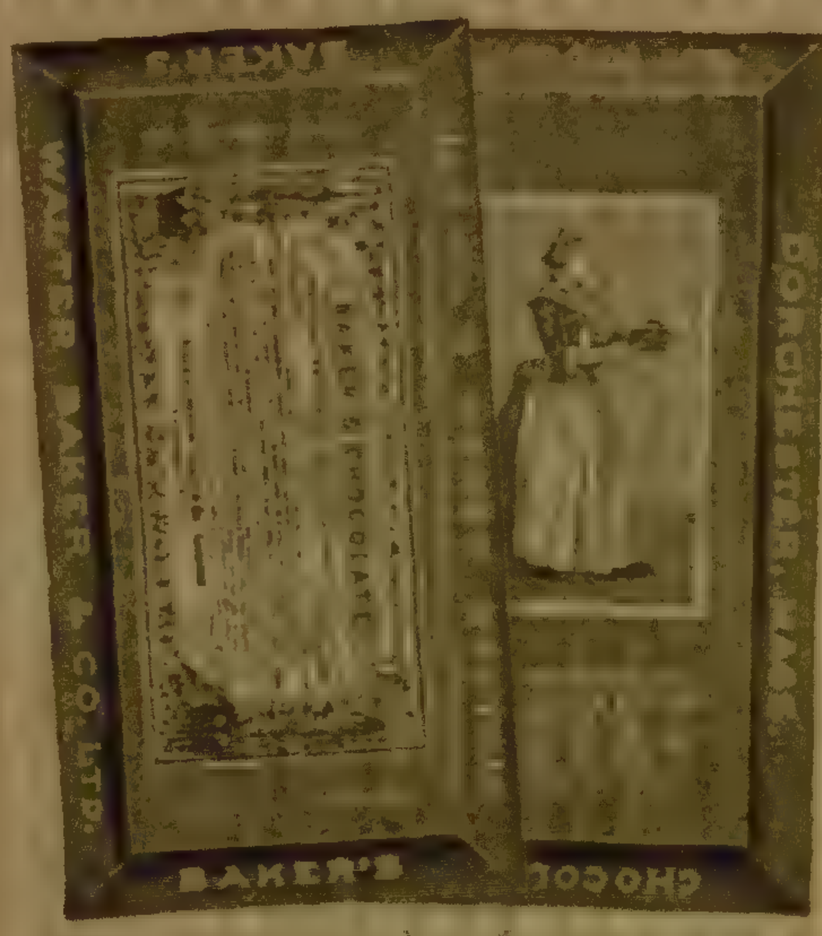

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THE BOTANICAL GAZETTE

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VOLUME LII NUMBER 3

THE

BOTANICAL GAZETTE

SEPTEMBER 1911

A PRELIMINARY REPORT ON THE YEARLY ORIGIN AND DISSEMINATION OF PUCCINIA GRAMINIS

FREDERICK J. PRITCHARD

(WITH PLATE IV)

Introduction

The annual reappearance of *Puccinia graminis* Pers., the black rust of cereals, and its dissemination among the various species of the Gramineae, have long remained obstinate problems. For nearly a century botanists and also agronomists, because of its economic importance, have endeavored to discover how this fungus passes the winter and spreads to the grain fields. A review of the literature, to bring out certain points which have been too much overlooked by those who are committed to the conception that the barberry is the sole source of spring infection, will be of interest in connection with the data which my own observations afford.

The barberry was considered a disseminator of rust by careful observers centuries ago. Even as early as 1660, as a result of their reports, an act of Parliament was passed at Rouen (**22**) condemning the use of this shrub in the vicinity of grain fields. A similar law was passed in Mass. (**28**) in 1755. Successive measures of this nature were subsequently enacted throughout Europe (**3**).

Proof of the influence of the barberry on rust contagion was furnished by SCHÖLER (**29**),[1] who in 1818 succeeded in infecting

[1] Cited by ERIKSSON.

rye with aecidiospores from barberry leaves. SCHÖLER's publication, however, remained buried until brought to light by NIELSON.

Infection of the barberry with *P. graminis* was not accomplished until 1865, when DE BARY (**3**) readily infected the young leaves with germinating sporidia, thus establishing the heteroecism of the organism. Unfortunately he was unable at the same time to germinate the mature aecidiospores, either fresh or after various periods of preservation, and hence the cereal host species was not reinfected, although the following year he accomplished this upon young rye plants.

The distance rust is spread from the barberry is variously estimated by different writers. MARSHALL (**24**),[2] who set large barberry bushes in the grain fields and made careful observations, states that the rust extended 10 yards in the direction of the prevailing wind. SCHÖLER (**29**), on the other hand, used small bushes and found that it scattered over an area of 30 to 40 square feet. Much greater distances are frequently recorded in the literature, although usually based upon casual observation or opinion. WITHERING (**33**),[3] for instance, advises that no barberry bushes should be planted within 300–400 yards of a grain field.

The absence of the barberry and *Mahonia* in several regions where *Puccinia graminis* is prevalent, as cited for Ecuador by LAGERHEIM (**21**), seems to indicate that the heteroecism of the fungus is merely facultative. According to BARCLAY (**1**), *P. graminis* is also commonly present in Jeypore, India, while the nearest barberry bushes are nearly 300 English miles distant. Moreover, "the aecidia are formed in summer, while the wheat and barley are grown in winter and harvested in April or May." In this same category ZUKAL (**34**) places Bosnia and Herzegovina, where, according to BRANDIS (**34**), the aecidial hosts, if present at all, are very rare. Perhaps the most striking case of this kind is in Australia, where *P. graminis* causes enormous damage to wheat, yet the barberry is not present and the aecidial stage has never been found.

The existence of a perennial mycelium, although established for a

[2] Cited by ARTHUR, Bull. Torr. Bot. Club **31**:113. 1904.

[3] Cited by ERIKSSON and HENNING (**16**).

number of rusts, has never been proved for *P. graminis*. ERIKSSON (**13, 14, 16**) found the mycelium scarcely extending beyond the contour of the pustules. DE BARY held that the development of the rust begins anew each year by the "germination of the teleutospores alone."

P. graminis was formerly considered one species capable of infecting various members of the Gramineae, and this supposedly wide range of infecting power was thought to conduce to its spread. ERIKSSON (**16**), however, after extensive inoculation experiments in Sweden, divides it into the following biological forms, which he finally classes as species:

Puccinia graminis secalis (Secale cereale, Hordeum vulgare, and Triticum repens).

Puccinia graminis avenae (Avena sativa).
Puccinia graminis tritici (Triticum vulgare).
Puccinia graminis airae (Aira caespitosa).
Puccinia graminis poae (Poa compressa).
Puccinia phlei-pratensis (Phleum pratense).

CARLETON'S (**10**) experiments in America, however, do not support ERIKSSON and HENNING'S results. He finds no distinction between the forms on wheat and barley. His results appear to establish two things: (1) "that the forms of black stem rust on wheat and barley, *Hordeum jubatum*, *Agropyron tenerum*, *A. Richardsoni*, and *Elymus canadensis glaucifolius*, are identical, with the probability that those on *Elymus virginicus muticus* and *Holcus lanatus* should be included; (2) that the black stem rust of *Agropyron occidentale* is physiologically distinct from any other."

Direct inoculation of the gramineous host with the germinating teleutospores has received some attention, although not as much as it deserves. Foremost among these experiments are probably those of DE BARY, who showed that the germinating sporidia of *P. graminis* would not infect the leaves of *Triticum vulgare*, *T. repens*, and *Avena fatua*. THÜMEN (**31**), however, asserts that the sporidia of *Melamspora salicina* infect the willow quite as easily as do the uredospores. PLOWRIGHT (**27**) also, in a detailed report, claims to have infected wheat plants directly with sporidia (teleutobearing straw), although he afterward informed KLEBAHN that

"his work rested upon an error." Other failures to infect wheat with germinating sporidia are reported by WARD (**32**) and ERIKSSON (**15**), though no mention is made of the number of trials nor the point of inoculation. Notwithstanding these failures, BREFELD (**8**) thinks further attempts should be made to infect young cereals with germinating teleutospores. His discovery that only the youngest tissues of cereals are penetrated by smut sporelings gives encouragement for numerous experiments in this direction. The hardened tissues may offer too much resistance to the delicate germ tubes of the sporidia, he says, which bore directly through the epidermis instead of entering through the stomata, as do the germinating uredospores and aecidiospores.

The behavior of the germinating teleutospores is influenced somewhat by their environment. MAGNUS (**23**) found that teleutospores of *P. graminis* kept under a thin layer of water formed a germ tube instead of a promycelium. These results were afterward confirmed by BLACKMAN (**5**), who also included two other genera. Other factors are sometimes operative, as KIENITZ-GERLOFF (**18**) reports that thin-walled teleutospores of *Gymnosporangium clavariaeforme* also form a germ tube. When teleutospores germinate in air, however, they almost invariably form sporidia. This is true of *P. graminis* even in Australia, where it has no aecidial host species.

The uredospores of *P. graminis* soon lose their viability, according to DE BARY (**3**), in one to two months if kept dry. BOLLEY (**6, 7**), however, obtained a germination of 5 per cent after exposing them to air and sunlight during the month of August, and even claims they may live over winter. Christman (**11**) failed to germinate them after November 23, although the uredospores of *P. coronata* were viable the 26th of January, and those of *P. rubigo-vera* the 21st of March. Perhaps the most extensive experiments of this kind have been made by ERIKSSON and HENNING (**16**), whose results show that the uredospores of both *P. graminis* and *P. glumarum* are unable to survive the winter in Sweden. The absence of fresh uredo pustules during two or three months in the spring is cited as additional proof, since the period of incubation after inoculation with uredospores is only about ten days. The

statement is also made by KLEBAHN (**19**) that "in Germany *P. graminis* does not appear to pass the winter as uredo." CARLETON (**9**) found this to be true in Kansas, and in a two weeks' trip through Texas in December 1895, he could find no rust on winter wheat or oats, although it was present there in abundance the previous summer.

The mycelium of the rust is not limited to the leaves and culms of cereals, but also enters the seed. ERIKSSON (**14, 16**) found it in abundance in the "peripheral tissues" of grains, but was unable to trace it into the young seedlings. ZUKAL (**34**) has made similar discoveries, and even found it in the seed coats of barley which was furnished by ERIKSSON and supposed to contain mycoplasm.

Spores of the Uredineae are frequently present in the seed of the host. SMITH (**30**) found teleutospores of *P. graminis* in oat grains lying next to the gluten layer, and ERIKSSON and HENNING (**16**) report the presence of both uredospores and teleutospores of *P. glumarum* in the pericarp of cereal grains.

Several rusts have been shown to infect their host species through the seed. CARLETON (**10**) demonstrated this conclusively for the *Euphorbia* rust (*Uromyces euphorbiae* C and P) with the seeds of *Euphorbia dentata*. The plants grown from disinfected seed were always free from rust, while the controls were heavily infected, although planted in sterilized soil and protected by bell jars. MASSEE (**25**) states that *P. malvacearum* Mont. commonly enters young hollyhock plants through the seed. According to MCALPINE (**26**) *P. beckmanniae* was introduced into Australia in 1903 and *P. impatientis* in 1904 through seed of *Beckmannia erucaeformis* and *Elymus condensatus*, respectively, received from the U.S. Department of Agriculture.

Experimental evidence seems to indicate that rusts may infect cereals through the seed. When oats were introduced into Ecuador by growing European seed in the botanical garden at Quito, LAGERHEIM (**21**) reports that the plants became heavily infected with *P. coronifera*, although neither this rust nor any of its aecidial hosts had ever been found in Ecuador. Carefully planned experiments, covering a period of years, were conducted by ERIKSSON (**15**) to determine whether *P. glumarum* winters in the seed of wheat

and barley. Glass cages of various sizes and types, provided with cotton ventilators to filter the air and caps to keep out the rain, were employed. Some were attached to a suction pump and artificially ventilated; others, on all sides except the north, were fitted with double panes of glass, between which was passed a continuous current of water. Despite all these efforts to produce a normal environment for the plants, the air inside the cages was always 2–6° degrees hotter than the air outside, and the light considerably diminished. The plants were always abnormal, often attaining two or three times the height of their outside neighbors. In a few cases a single winter cereal plant was placed in each of several glass tubes early in the spring, long before any rust appeared outside. As a rule, however, seeds were planted in pots of sterilized soil and placed in the bottom of the cages. As all the air entering the cages passed through cotton filters, no spores could be carried in from the outside. Although the majority of his results were negative, a considerable number of infections was obtained with both winter cereals and annuals. This he considered fully as much as could be expected, since the plants were grown under abnormal conditions. A similar set of experiments was planned by MASSEE (**25**), who planted wheat seed infected with *P. rubigo-vera* in two pots of soil and kept them covered with bell jars provided with cotton wool filters. In one pot 26 per cent of the plants rusted, and in the other 47 per cent, while not a pustule appeared on the controls.

The amount of rust developing in the grain field seems to vary somewhat with the date of sowing. Both the early and late grain, according to ERIKSSON and HENNING'S tables for the different cereals, are usually less rusty than those sown at an intermediate date. GALLOWAY (**17**) called attention to this fact in 1893, when all his duplicate plots of grain, sowed ten days later than the originals, were free from rust. Moreover, he says, "Examining the weather records for ten days preceding the rust, we find nothing to warrant the belief that the simultaneous appearance of the fungus the first week in May in widely separated spots was due to peculiar climatic conditions."

ERIKSSON'S well known mycoplasm theory was advanced to

explain such cases. This theory is based chiefly upon the claim that rust apparently infects the cereal host through the seed, although its mycelium is not recognizable in the germ by aid of the microscope and present cytological technique. KLEBAHN (**20**), for a time at least, supported this view, and even figured the nuclei of the fungus while in the mycoplasmic condition.

The following experiments on the life history of *P. graminis* were made at the North Dakota Agricultural College and Experiment Station at Fargo, North Dakota, to obtain information which would aid in producing a rust epidemic yearly in our wheat breeding plots to test the strains selected for rust resistance. This is a spring wheat region, where the winters are exceedingly cold and consequently winter cereals are not grown.

The germinating rusted wheat grains were studied at Madison, Wisconsin, under the direction of Dr. R. A. HARPER.

Method

All the plants used for inoculation, except when otherwise stated, were grown in the greenhouse in beds containing 6–8 inches of fertile soil. The grass plants were transplanted to pots and placed in the greenhouse several weeks before they were used. The temperature was kept reasonably cool, and the air fairly moist by frequently watering the floor.

The inoculations were made by first mixing the spores of a pustule in a small quantity of distilled water. The plants were then moistened with distilled water by means of an atomizer and the spores applied with a camel's hair brush. Except in a few cases where the plants were very large, they were kept under bell jars 24–48 hours. If they became dry, they were sprayed again the second day. Generally, however, they were quite moist when the covers were removed. For part of the work inverted test tubes attached to stakes at suitable heights were employed, the lower end being lightly closed with cotton wool. The test tubes were found to retain the moisture even better than the bell jars. Parallel marks were sometimes made on the leaves by means of India ink and the spores placed between them. The

beds containing these plants were generally watered just before making the inoculations, to provide a source of moisture for the air beneath the covers. When not stated, the height of the plants on which bell jars or test tubes were used varied from 8 to 13 inches, without straightening up the leaves.

The wheat seedlings, grown from the rusted seed at Madison, Wis., and sectioned for study, were killed and fixed in Flemming's strong solution, imbedded in paraffin, and stained with either iron-alum hematoxylin or the triple stain.

Experimental investigations

Experiments were begun to show how readily sporidia of *P. graminis* from wheat and native grasses infect the barberry, although there are very few barberry bushes in North Dakota, so few in fact that they could hardly be considered as a source of rust epidemics, unless miraculous powers were attributed to the wind in causing a widespread and uniform distribution of aecidiospores. In the following experiments small pieces of dead straw, which were covered with teleutospores of *P. graminis* and had lain on the ground during the winter, were arranged parallel to each other and tied longitudinally on the branches of the barberry bushes (*Berberis vulgaris*), just as the buds were beginning to unfold in the spring.

TABLE I

INOCULATION EXPERIMENTS WITH TELEUTOSPORES OF *Puccinia graminis* Pers.

Number of experiment	Date of inoculation	Source of material	Number of branches inoculated	Results
5	April 30, 1906	Agr. ten.*	5	5 positive
6	April 30, 1906	Agr. ten.	7	1 positive
7	April 30, 1906	Wheat	2	2 positive
9	April 30, 1906	Agr. rep.	2	2 positive
10	April 30, 1906	Wheat	1	1 positive
11	April 30, 1906	Hord. jub.	2	2 positive
12	April 30, 1906	Ely. trit.	2	1 positive
13	April 30, 1906	Wheat	1	1 positive
14	May 2, 1906	Wheat	3	3 negative

* Abbreviations: Agr. ten. = *Agropyron tenerum;* Agr. rep. = *Agropyron repens;* Hord. jub. = *Hordeum jubatum;* Ely. trit. = *Elymus triticoides;* Ber. vul. = *Berberis vulgaris*.

In experiments 5–13 inclusive, the inoculated barberry branches were heavily infected the 14th of May. Only spermagonia were present on this date, but they were frequently on both surfaces of the leaves. There were a few spermagonia on other parts of the bushes, but no such dense blotches as appeared where the rusty straw was applied.

Further inoculations were made upon the barberry by scraping the teleutospores from dead straw, wintered the same as that described for Table I, and placing it on young buds or leaves which were carefully marked off by India ink and tagged. These results are recorded in the following table.

TABLE II

INOCULATIONS MADE UPON *Berberis vulgaris* WITH TELEUTOSPORES FROM *Puccinia graminis* Pers.

Number of experiment	Date of inoculation	Source of material	Number of parts inoculated	Results
19	May 8, 1906	Oats	10 buds	10 negative
22	May 9, 1906	Ely. trit.	10 buds	2 positive
27	May 21, 1906	Ber. vul.	10 buds	10 negative
28	May 22, 1906	Wheat	8 leaves	8 positive
52	June 26, 1906	Ely. trit.	1 leaf	negative
53	June 26, 1906	Hord. jub.	1 leaf	negative

As shown by the table, these results were mainly negative, perhaps on account of poor germination, since the buds selected were fully as young as those used earlier.

In order to obtain pure cultures of aecidiospores of known origin for further experiments relative to their infecting power, inoculations were made upon barberry bushes which had been standing in the greenhouse in large tubs for nearly a year and had borne no rust. The infections were made by tying small pieces of old rusty straw on the bushes in places offering the least opportunity for contamination and moistening the straw frequently with distilled water. A summary of the results is shown in Table III.

Aecidia appeared only on parts of the barberry inoculated, and, with the exception of the rusty oat straw from which all my inoculations so far have failed, infections were obtained from each kind of material. This with the data of the two preceding

tables shows that under favorable conditions *P. graminis* passes readily to the barberry from wheat and certain grasses, viz., *Agropyron tenerum*, *A. repens*, *Hordeum jubatum*, and *Elymus triticoides*, confirming the general results of DE BARY and others.

TABLE III

INOCULATIONS MADE UPON *Berberis vulgaris* WITH TELEUTOSPORES OF *Puccinia graminis* Pers.

Number of experiment	Date of inoculation	Source of material	Method	Results
1	March 29, 1907	Agr. ten.	Bell jar	Positive
2	March 29, 1907	Agr. ten	Bell jar	Negative
3	March 29, 1907	Agr. rep.	Bell jar	Positive
4	March 29, 1907	Agr. rep.	Bell jar	Negative
5	March 29, 1907	Oats	Bell jar	Negative
6	March 29, 1907	Oats	Bell jar	Negative
7	March 29, 1907	Oats	Bell jar	Negative
8	March 30, 1907	Wheat	Bell jar	Positive
9	March 30, 1907	Wheat	Uncovered	Negative
10	March 30, 1907	Hord. jub.	Bell jar	Positive
11	March 30, 1907	Hord. jub.	Uncovered	Negative
12	April 4, 1907	Wheat	Uncovered	Negative
13	April 4, 1907	Wheat	Uncovered	Negative

Observations were made on the dissemination of rust from barberry bushes by taking note of the infection on the surrounding grasses. There was a small barberry hedge in Fargo very favorably located for this purpose, as it was surrounded on three sides by meadow and was heavily rusted every year. Careful observations for three successive springs (1905–1907) furnished some surprising data. Early each year, the plants of *Hordeum jubatum*, *Agropyron repens*, and *A. tenerum* in the immediate vicinity of the hedge became thoroughly covered with the uredo stage, while *Phleum pratense* and *Poa serotina* were absolutely free from it, and *Elymus virginicus* bore only an occasional pustule. The rust was abundant within 25 yards of the barberry bushes, but practically disappeared at a distance of 60 yards. The most persistent searching was required to discover a single pustule beyond 80 yards, and in no one of the three springs at this early date, before rust had begun to spread from the uredospores, could I find fresh uredo pustules of *P. graminis* beyond 100 yards from the barberry hedge, notwithstanding the fact that in 1905 rust was fairly abun-

dant in this region. Either the aecidiospores are not borne as great distances by the wind as formerly supposed, or their germinative power is remarkably low. There is some additional evidence in support of the latter view.

Plots of small wheat plants in the experimental garden were sprayed repeatedly with aecidiospores in the spring of 1905, yet scarcely any rust appeared until the plants were nearly two feet high, a fact commonly observed here in the field every spring, although volunteer wheat plants barely out of the ground in the fall are often covered with rust.

Two series of infection experiments were made to obtain further data with reference to the spreading of *P. graminis* by means of its aecidiospores. From 98 aecidial pustules, taken at random in 1906, a total of 368 plants were inoculated. Plants of wheat, rye, oats, barley, and usually *Avena fatua*, *Agropyron tenerum*, *A. repens*, and *Hordeum jubatum* were inoculated from each aecidial pustule and covered with bell jars 24–48 hours. Germination tests of the spores, made by placing them in water and on wet filter paper kept in a moist chamber at 18–20° C., showed a viability of about 8 per cent. Rust appeared only on *Avena fatua*, *Agropyron repens*, rye, oats, and *Hordeum jubatum*. No plants of barley or wheat were infected. These experiments were repeated in 1907 by inoculating 247 plants from 13 pustules of known origin, the original host species always being included in each group. Tests of the spores showed about the same percentage of germination as those used in the former experiments. No barley plants were infected, and the only wheat plants which developed rust were those inoculated with a form which came originally from wheat. The aecidiospores of only 9 pustules, however, of the 111 used in the two series of experiments caused infection. This relatively low number of infections agrees with the results obtained by repeatedly spraying the wheat plots with aecidiospores in 1905, and may partly account for the confining of the rust to the immediate vicinity of the barberry hedge as observed for the three successive years 1905–1907. It is also in harmony with the very limited spreading observed by both MARSHALL and SCHÖLER when they set barberry bushes in the

grain fields, and might easily be accounted for by the change of host species if the heteroecism of the fungus is only facultative.

A suspicion has frequently been expressed that the black rust spreads to the grain fields by aid of the grasses which either harbor the mycelium over winter or are infected early by aecidiospores. In order to determine the interval between the appearance of rust on grasses and cereals, the following observations were made in the spring of 1905. Rust the following summer, although not as abundant in North Dakota as in 1904, was still quite pronounced.

TABLE IV

FIRST APPEARANCE OF *Puccinia graminis* Pers. UPON GRASSES AND CEREALS AT FARGO, NORTH DAKOTA, IN THE SPRING OF 1905

Date of observation	Host species	Spore pustules	Location	Remarks
June 27..	Hord. jub.	Uredo	Grass garden	A few pustules on a single plant
June 29..	Hord. jub.	Uredo	Near barberry	
July 6 ...	Spring wheat	Uredo	Field	Far removed from barberry bushes.
July 9....	Agr. rep.	Uredo	Near barberry	Present in abundance on both Agr. rep. and Hord. jub. None found elsewhere although a diligent search was made.
July 10...	Winter wheat*	Uredo	Field	Found in abundance at a considerable distance from barberry bushes.
July 12...	Agr. rep.	Teleuto	Near barberry	Present on both Agr. rep. and Hord. jub.
July 13...	Winter wheat	Teleuto	Field	Same plot of winter wheat mentioned above.
July 16 ..	Spring wheat	Uredo	Field	Appearing quite generally on all the oldest wheat.

* This was an experimental plot of winter wheat in charge of Dean J. H. SHEPPERD, the agronomist, and the writer was not aware of its presence until July 10, when the plants which had survived the winter were thoroughly covered with mature uredo pustules of *P. graminis*, some quite old, the rust having first appeared probably 10–14 days earlier.

The foregoing table shows that *P. graminis* probably appeared upon the experimental plot of winter wheat almost or quite as early as upon *Agropyron repens* and *Hordeum jubatum*, even when the latter were in the immediate vicinity of the barberry. It also shows that, with the exception of the one case mentioned

under date of June 27, the uredospores of *P. graminis* were generally present upon the spring wheat earlier than they were observed upon the wild grasses remote from the barberry bushes. In fact, *P. graminis* was present in the uredo stage upon spring wheat July 6, and with one exception could not be found upon the grasses remote from the barberry even July 9, after which date no further search was made for uredo upon the latter.

Experiments were made to obtain data with reference to the spread of *P. graminis* from grasses to the wheat fields by means of the uredospores. Twenty-eight uredo pustules were selected from *Agropyron tenerum*, *A. repens*, *Avena fatua*, and *Hordeum jubatum*, and 230 plants inoculated. From each pustule inoculations were made upon plants of wheat, barley, rye, and oats, and upon the host species from which the rust was obtained. Parallel marks were made upon the leaves with India ink, and the spores placed between them in order to distinguish the results of regular inoculations from accidental infection. There was very little spreading of the rust, however, as the infected leaves were always removed from the greenhouse. The plants were covered with bell jars 24–48 hours, as formerly. Germination tests of the uredospores showed an average viability of 70–80 per cent.

The uredospores of 21 of the 28 pustules caused infection, but showed a decided preference for certain host species. The rust readily infected rye, oats, and the grasses, but not wheat or barley. In fact, the results of the few experiments made seem to show what was anticipated from the two series of infection experiments with aecidiospores, viz., that one form of *P. graminis* is common to *Hordeum jubatum*, *Agropyron tenerum*, *A. repens*, *Avena fatua*, oats, and rye, but is incapable of infecting either barley or wheat. This furnishes little encouragement to those who believe that *P. graminis* is spread to the wheat fields from the barberry bushes or from occasional protected spots, as beneath ice by aid of the native grasses. The data however give no information with respect to the forms of *P. graminis* on wheat or barley, as neither was infected, but in our breeding experiments in 1905 a number of wheat plots were surrounded by a border of barley which was practically destroyed by black rust, and yet there was no visible

evidence that it ever spread to the wheat. Hence it appears that the forms upon these two species are distinct.

The wintering of *P. graminis* as mycelium in plant tissues in North Dakota is extremely doubtful, as there are no winter cereals and the uredo stage does not appear upon the grasses until very late in the spring, when they are quite large. To test the supposition, however, that the fungus might pass the winter in occasional plants under shelter and produce a new outbreak of uredo the following season, I placed heavily rusted plants of *Agropyron tenerum*, *A. repens*, *Hordeum jubatum*, *Elymus virginicus*, and *E. canadensis* in large pots three successive falls (1904–1907) and transferred them to the greenhouse where they remained until summer, but no fresh uredo pustules ever appeared on any of them. Furthermore, in collecting data relative to the appearance of *P. graminis* upon cereals and grasses in the spring of 1905, a piece of low meadow containing *Hordeum jubatum*, *Agropyron tenerum*, and *A. repens*, which was flooded by the city in the winter and used as a skating pond, was carefully observed, but no uredo pustules appeared here until they were found on the grains and grasses elsewhere.

The origin of spring infections has frequently been attributed to over-wintered uredospores, although this is merely a hypothesis. In order to determine with some accuracy the duration of the germinative capacity of the uredospores of *P. graminis*, the following experiments were made. Bundles of rusty straw which had stood in the shock until late in the fall of 1904 were placed on the ground. Others were tied to trunks of trees, and some stored in the attic of one of the college buildings, where the temperature was below freezing but much warmer than the outside atmosphere. Rusty wheat straw was also put in manila envelopes and in test tubes, and these laid in pasteboard boxes on the ground. All the material placed upon the ground was covered by snow the greater part of the winter. To still vary the conditions, test tubes of rusty wheat straw were attached in an inverted position to stakes outside, 2–3 feet above the ground, while packets were buried in ice at the ice house and others kept in the laboratory. From the middle of September to the following July germination tests of the uredospores were made once a week from all these sources. At

the beginning of the experiment, about 10 per cent of the uredospores were viable, but by the end of September this had dwindled to 2 per cent; and only an occasional uredospore germinated in October and none whatever after November 15.

Some confusion arose at first over a fungus whose hyphae emerged from the germ pores, but without showing any conspicuous evidence of its entrance. This fungus proved to be an *Alternaria*, which parasitized many uredospores.

Repeated attempts were made to germinate uredospores from *Hordeum jubatum* and occasionally from *Agropyron repens* which were buried under ice and snow, but always without success. Old uredospores can be obtained in abundance all winter and in early spring on *Hordeum jubatum*, lying between the stem and sheath, but it is practically impossible to find them here on other grasses in winter, although the plants may be buried under ice in low places, as they drop off before winter and are replaced by teleutospores. Hence no uredo pustules were available from other grasses except *Agropyron repens*, whose few winter-borne uredospores would not germinate.

The germination tests show that during the winter of 1904–1905 in North Dakota all or practically all the uredospores of *P. graminis* probably lost their viability, and hence were not the cause of the large amount of black rust in the state the following summer.

The annual reappearance of *P. graminis* in Kansas, Nebraska, and the Dakotas has often been explained by assuming that it passes the winter in Texas and spreads north by means of the wind and growing crops. To obtain data on this point an endeavor was made to catch uredospores of *P. graminis* from the air before any pustules appeared upon the wheat. A post 5 feet high was set in the edge of a wheat plot and a soup dish 7 inches in diameter, containing a small quantity of distilled water, just enough to fill one tube of the centrifuge, was exposed at its top 30–40 minutes. The whole inner surface of the dish was rinsed with the water to collect any spores adhering to its sides. The water was then poured into a tube provided with a tapering bottom, and the débris precipitated by means of a centrifuge. All the particle-bearing liquid was removed from the narrow end of the tube by

means of a pipette, placed upon six slides and examined microscopically. This process was repeated two or three times a week for nearly a month, but no uredospores of *P. graminis* were caught until uredo pustules were abundant on the surrounding wheat.

Further observations were made to determine whether uredospores are commonly borne very great distances by the wind. On a piece of ground one-third to one-half acre in area, which we used for breeding rust-resistant wheat, a rust epidemic was produced every year. This was accomplished by plowing into the soil rusty wheat straw and spraying the wheat repeatedly with aecidiospores of *P. graminis tritici* Erik. and Henn. It should also be mentioned that our original seed, the foundation stock, was obtained from the badly rusted crop of 1904. Hence there were present teleutospores, aecidiospores, uredospores, and probably infected seed. For the present, however, we are concerned only with the fact that rust annually appeared upon these plots in great abundance. In fact it was almost impossible to obtain any plump kernels of wheat from plants grown here. During at least two summers (1906–1907), when these plots were thoroughly covered with *P. graminis*, there was scarcely any rust on the field plots of wheat which lay a short distance north of the infested area and in the direction of the prevailing winds, although the latter passed over the breeding plots, often causing considerable annoyance while I was taking rust notes. The only possible hindrance to the passage of the spores was a few rows of shrubs covering a strip about 10 feet wide, thinly planted and varying from 6 to 8 feet in height, located 20–25 yards from the rust bed. However, there was a road about 20 feet wide running north and south through the shrubbery and along the west edge of the infested area. Hence there was ample opportunity for wind distribution of the uredospores, and former experiments have shown that they were highly viable during the summer of 1906, yet practically no rust appeared upon these neighboring wheat plots. The fact that *P. graminis* does not appear upon wheat in North Dakota in the summer until the plants are nearly 2 feet high, several weeks after the wheat crop is harvested in Kansas and Nebraska,

would also appear to indicate that the spores are not commonly borne very great distances by the wind.

Little or nothing has been done in the past to test the possible infection of sprouting cereals by means of germinating teleutospores from the soil. When buried in moist earth it is not even known whether teleutospores can produce germ tubes or promycelia. A striking fact in connection with the possible infection of seedlings by teleutospores was observed in our field work. Our breeding ground, in which we produced an abundance of rust annually as described above, consisted in 1907 of three parts which, however, were not separated by paths or any visible marks. The whole west half had grown three successive crops of rusted wheat (1905–1907); all the east half except a narrow strip on the north end grew rusted wheat in 1905 and 1907, but produced a crop of flax in 1906; the remainder was in sod until 1907, when it was planted to wheat. The rusty wheat instead of being removed from the ground was always plowed under. The same varieties, except some of Farrer's wheat which was not taken into account, were planted on all three areas at the same dates. The soil was equally level and very fertile. All the wheat was inoculated alike during the spring and summer of 1907, yet shortly before harvest the three parts were separated quite distinctly by lines of rust demarkation, the amount of rust varying with the number of crops of rusted wheat grown upon each area. Whether these results are due to the different quantities of teleutospores in the soil of the different areas or not cannot of course be definitely stated, but they are at least suggestive of the need of further experiments in this direction. If the perpetuation of the wheat rust in the absence of the barberry is due to the teleutospore infection of the germinating seed, variation in the time of seeding might easily account for the annual variability in its prevalence.

The further possibility that rust may be carried in the seed itself is certainly also to be considered. Teleutospores and mycelial fragments of *P. graminis* are often present in abundance in the pericarp of wheat grains, and can frequently be recognized by the appearance of pustules, as will be described later. Early in the spring of 1905 about 60 wheat grains with such contamination

were planted under each of two glass cages provided with cotton ventilators to prevent the entrance of spores from the air. The experiment was afterward repeated in the greenhouse, but rust never appeared on the plants in either case. The conditions however were exceedingly abnormal. The ventilators were entirely too small and the moisture inside the cages was always excessive. While the plants grew rapidly, headed, and blossomed, they failed to set seed both years. Another experiment made in the spring of 1905 appeared to give more favorable results. Wheat was sowed at various dates, some of it quite late. It was all inoculated early and repeatedly with both aecidiospores and uredospores of *P. graminis tritici* Erik. and Henn., the latter being obtained chiefly from the experimental plot of winter wheat of the same source as noted above, but the wheat of every sowing remained nearly free from rust until it began to head, when each in turn became thoroughly rusted. It might be assumed on this evidence that wheat has only a definitely limited period of susceptibility, still very small volunteer wheat plants are often quite rusty in the fall. It is possible to attribute this peculiar behavior to infection through the seed with a long subsequent incubation period in the growing plant, although the possibility of its coming through the soil is not excluded.

The infection of wheat grains with *P. graminis* can often be recognized by the presence of a tiny black spot where the grain separated from the mother plant. When black, this area is generally filled with teleutospores, which can be distinguished in mass with the naked eye or at least with the aid of a hand lens. Such grains are usually shrivelled, but occasionally they remain quite plump. Grains showing a spot of larger area with somewhat irregular boundaries are usually infected with other fungi, as *Alternaria* or *Helminthosporium*, and may not even contain rust. These are the so-called "black-points" mentioned by BOLLEY.[4]

In rusted grains of wheat the pustules are usually most abundant in the thick portion that was formerly attached to the rachilla, but they are also found in other parts of the pericarp, and often lie in the seed coats where they are pressed against the endosperm

[4] Science, Oct. 21, 1910, p. 1.

or embryo. As many as 10 pustules are sometimes seen in a single section, and nearly all of them are wholly inclosed by the tissues. All about the pustules are masses of rust mycelium, but the hyphae are not confined to these areas. They extend considerable distances from the pustules, and are present in numerous grains in which teleutospores cannot be found.

To obtain further information relative to infection through the seed, badly rusted grains of wheat after germinating from one day to two weeks were studied in the botanical laboratory at Madison, Wis., by means of cytological methods. The seed available was a remnant of former experiments, 4 or 5 years old, and revealed some very interesting phenomena.

Teleutospores in certain pustules, lying in the region of the hilum, were found to be undergoing remarkable changes, resembling the so-called palmella formations of certain filamentous algae. The protoplasts appeared to grow and divide in various directions, often distending the walls until they became quite thin (figs. 5–13). The nuclei, though not well fixed, were present as irregular densely stained bodies. Frequently one or both cells of the teleutospore were still undivided (figs. 1–3, 15), but numerous later stages were present, in which the protoplast had divided one to several times. As a rule, the wall between the two original cells was quite thin and persisted for some time (figs. 5, 6, 8), but occasionally it could not be distinguished (fig. 7). In the latest stages observed the cells became more distinct, often rounding slightly and acquiring thicker walls (figs. 7, 8, 11, 12). A view of the apical end of the teleutospore represented by fig. 12 is shown in a lower focus in fig. 11. In numerous cases the two halves of the former teleutospore finally separated from each other, forming two more or less globular multicellular aggregates (figs. 13*a*, 18). That these conditions are due to a parasitic mycelium, which has penetrated the teleutospores and completely replaced the protoplasts of the rust, is of course a possibility to be reckoned with. As is seen from the figures, however, direct evidence of the presence of such a parasite is entirely lacking. There is no mycelium outside the rust cells, and no evidence of a gradual absorption and replacement of the rust protoplast by that of a parasite. The subsequent

behavior of the cells will of course show their true nature, but as material is not available for following them through the later stages of germination of the seedling, it seems best to publish as a preliminary account the figures of the stages already found. The importance of their bearing on a possible method of wintering of wheat rust in the absence of the barberry or uredo is apparent.

These peculiar phenomena were not confined to the teleutospores, but were frequently present in the stalk cells (figs. 2, 5, 9, 10), and even in the mycelial region below (figs. 14, 15). Fig. 14 represents a radial section through the base of a pustule, one teleutospore and neighboring stalk cells being included. As is seen, the growing cells of the sorus were associated more or less in groups, but usually interspersed with smaller empty cells. Sometimes they formed dense areas, where it was difficult to determine whether they were of hyphal or teleutosporic origin. Now and then faint outlines resembling distorted, multicellular teleutospores were seen in the mass, but in all probability at least some of the cells arose from the mycelium. Apparently identical cells were found in other parts of the pericarp remote from the pustules (fig. 17). Lying near were filaments composed of similar though usually smaller cells (figs. 16, 17, 19). These however were enlarged portions of a smaller mycelium, all the remaining cells being empty.

Quite separate from the cells just described, fragments and often considerable pieces of what appeared to be living rust mycelium were found mixed with dead hyphae of the rust (figs. 20–22). They were usually in the pericarp, but often lay next to the deepest layer. There were occasional places outside the region occupied by the layer of feeding cells where they passed through into the cells of the scutellum and were found in considerable abundance within 6 or 7 cells of the growing plant itself (fig. 21).

As noted, the fate of the teleutosporic and mycelial cells described above remains for future determination, as my present material contains no later stages. The evident suggestion is that they may serve as growing points for the development of new rust mycelia and the infection of the embryo and seedling.

The possibility for infection of the seedling when the pericarp

of the seed is filled with living rust would seem to depend chiefly on the presence of reserve food for the fungus and the capacity of the hyphae to grow through a few dead cells. The penetration of the dead tissue may and probably does offer some difficulty to the majority of the hyphae, but in some places only a single cell wall of the pericarp intervenes, which could scarcely be looked upon as an absolute obstruction. At any rate, an abundance of mycelium resembling rust was found in the scutellum close to the growing tissue, with apparently nothing to hinder its further progress in that direction.

Whether after infection of the embryo in the manner suggested the rust mycelium might grow with the plant and take on a virulent form at later stages, when it spreads to form pustules, is certainly an interesting possibility. Such a general systemic infection was assumed in ERIKSSON'S mycoplasm theory, and there is some evidence in the general behavior of the rusts as noted above to suggest such a possibility. That such a palmelloid growth of fungal hyphae under peculiar conditions of nutrition is to be expected is abundantly shown by RACIBORSKI'S interesting observation on a palmella-like growth of *Basidiobolus* when placed in media rich in nitrogen. Further investigation of the infection of wheat by rust through the seed will be made when suitable material is obtained.

Summary

1. *Puccinia graminis* passed readily from wheat, *Agropyron tenerum*, *A. repens*, *Hordeum jubatum*, and *Elymus triticoides* to the barberry.

2. Observed facts seem to oppose the theory that aecidiospores and uredospores are carried considerable distances by the wind.

3. Uredo pustules of *P. graminis* appeared upon the experimental plot of winter wheat as early as upon grasses near the barberry bushes, and with one exception were generally present upon the spring wheat earlier than they appeared upon the grasses remote from the barberry.

4. *P. graminis* does not appear to spread to the wheat fields by aid of the grasses. The few experiments made seem to show three distinct biological forms of this fungus: one for wheat, one

for barley, and one for rye, oats, *Hordeum jubatum*, *Agropyron tenerum*, *A. repens*, and *Avena fatua*.

5. Uredospores of *P. graminis* failed to survive the winter of 1904–1905 at Fargo, North Dakota.

6. The wintering of *P. graminis* as mycelium in plant tissues in North Dakota is very doubtful, as shown by the late appearance of the uredo pustules in the spring and the failure of rusted grasses to produce the uredo again after being housed during the winter.

7. The pericarp of rusted wheat grains is frequently filled with rust mycelium and numerous pustules of teleutospores.

8. Teleutospores in some of the germinating grains appeared to be germinating in a palmella-like stage.

9. Pieces of mycelium resembling rust were found in the cells of the scutellum close to the growing plant.

In conclusion, I wish to acknowledge my indebtedness to Dr. R. A. HARPER for aid in the cytological study of the material and in the preparation of the paper.

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EXPLANATION OF PLATE IV

Phenomena appearing in the mycelium and teleutospores of *Puccinia graminis* in rusted grains of wheat during germination:

FIGS. 1, 2.—Teleutospores, showing thin walls and cells preparing for division; fig. 2 also shows an enlarged distorted stalk cell in which a cell wall has been formed.

FIG. 3.—A teleutospore whose lower cell has divided.

FIGS. 4–6, 9, 10.—Early palmella-like stages, showing angular cells with thin walls.

FIGS. 7, 8, 11, 12.—Late palmella-like stages, in which the cells are more or less rounded, thicker walled, and less crowded.

FIG. 13.—A group of teleutospores lying in the edge of a pustule that was sectioned somewhat obliquely.

FIGS. 14, 15.—Radial sections through the base of pustules showing living cells of the sorus.

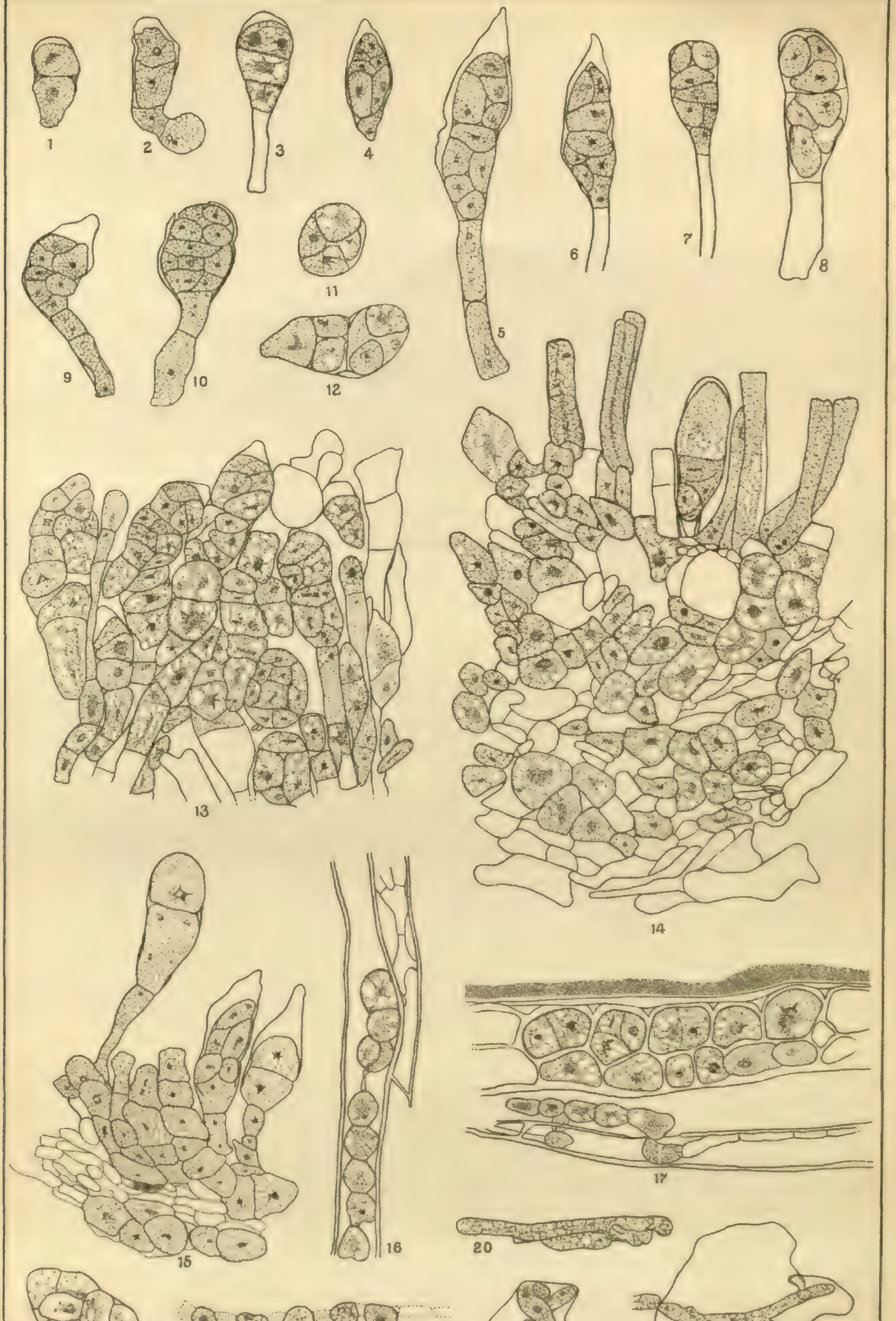
FIG. 16.—Mycelium lying in the pericarp; a few cells were alive and considerably enlarged, while the remainder of the filament was dead.

FIGS. 17, 19.—Dividing cells and living portions of mycelium lying in the pericarp remote from pustules; as in fig. 16, only a small portion of each filament was alive.

FIG. 18.—A group of cells found among the teleutospores of a pustule similar to that represented by fig. 13 (cf. 13*a*).

FIGS. 20, 22.—Fragments of mycelium found in the pericarp mixed with dead hyphae of the rust.

FIG. 21.—A typical piece of mycelium found in the scutellum within 6 and 7 cells of the radicle.



PRITCHARD on PUCCINIA GRAMINIS

EVAPORATION AND PLANT SUCCESSION[1]

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 147

GEORGE DAMON FULLER

(WITH SIX FIGURES)

The plant associations on the sand dunes of Lake Michigan have been described by COWLES (1), who has called attention to the succession which is here so strongly marked and so easily determined. In much of the region immediately south of the lake, the forest succession consists principally of associations dominated respectively by cottonwood, pine, black oak, white and red oak, and beech in the order named. These are usually designated the cottonwood, pine, and oak dunes, and the oak-hickory and beech-maple forests. They represent the major associations in a succession extending from the pioneer trees to the climax mesophytic forest formation of the region. The dynamic physiography and the details of the composition of the various stages in the succession have been so thoroughly discussed by COWLES that little further elucidation is necessary, but hitherto no attempt has been made to obtain any quantitative determination of any of the factors influencing this succession.

The researches of LIVINGSTON (2) and others have shown that the evaporating power of the air is a rather satisfactory summation of the atmospheric factors which determine the growth of plants during that portion of the season free from frost, and that it can be accurately measured by the porous-cup atmometer; accordingly, in the spring of 1910, a number of observation stations were established upon the sand dunes near Millers, Ind., and the rate of evaporation was determined during the ensuing growing season. Both the porous-cup atmometer devised by LIVINGSTON (3) and the type described by TRANSEAU (4) were employed in this investigation. They were mounted in wide-mouthed bottles having a

[1] A preliminary report of evaporation studies in the plant associations upon the sand dunes of Lake Michigan.

capacity of 500 cc., closed with tightly fitting cork stoppers that were perforated for the atmometer tubes and for bent capillary glass tubes which served to equalize the atmospheric pressure within the bottles with that of the exterior air, without causing any loss by evaporation or permitting rain water to enter the reservoir. The bottles were sunk in the soil about two-thirds of their height, so that the evaporating surface of the instruments was 20–25 cm. above the surface of the soil. Except where otherwise specified, the readings were made weekly by filling the bottles from a graduated burette to a file scratch on the neck. The small area of the water surface at this point made the probable error in readings less than ±0.5 cc., and this could have had no appreciable effect upon the results. The instruments were all standardized to the same unit before being used, restandardized at intervals of 6–8 weeks during the season, and a final correction made on their being collected in the autumn. By the coefficients thus obtained all readings were reduced to the standard adopted by LIVINGSTON (**5**) in his recent paper on the operation of the porous-cup atmometer. The directions given in that article were so closely followed that it is unnecessary to detail further the methods used in operating the instruments. Two or three atmometers were discarded during the season on account of various irregularities in their operation, but others either maintained a uniform rate of water-loss or showed a variation that progressed uniformly at a readily calculable rate. To provide still further against the possibility of serious error, two instruments were often maintained a few feet apart at the same station, and several stations were usually established in the same association, the mean of the various readings being taken as giving the true measure of the evaporating power of the air for that association.

No correction has been made for errors caused by rainfall, although during showers some water undoubtedly passes through the porous cup and into the reservoir, because it was thought that the amount of variation thus produced would be the same for all stations within so limited an area, and hence the comparative relation of results would remain unchanged. This assumption has been largely verified by BROWN (**6**), using an atmometer with a rain-

correcting valve. It is the intention of the writer, however, to employ this improved atmometer, also devised by LIVINGSTON (**7**), in the continuation of these studies.

Fifteen different stations were established in the various associations, care being taken to select spots which possessed the average amount of tree, shrub, and herbaceous vegetation characteristic of that specific association as a whole. Owing to a variety of accidents and other circumstances, all the stations did not give equally satisfactory and continuous records; hence the present preliminary report is confined almost entirely to the results from 10 stations in 4 different associations. Many of these records extend from May 6 to October 31, or over a period of 178 days; at other stations the record begins at a somewhat later date, but continues until the severe frosts of November 1, and includes the important part of the growing season for all except a few very early spring plants.

In order to facilitate comparisons between the various stations, and to exhibit the progress of the evaporation rate during the entire season, the average water-loss per day between the weekly readings has been calculated, and the results expressed in graphs with ordinates representing the number of cubic centimeters lost per day by a standard atmometer, the abscissae being the intervals between the weekly readings. The readings included within each calendar month are indicated at the top of the diagram. For convenience of reference, the stations are numbered consecutively, beginning with that nearest the lake shore.

The first group of stations was upon some slowly moving dunes directly north of the village of Millers, Ind., and between the southern shore of Lake Michigan and the Grand Calumet River. According to old maps, this river formerly discharged its waters into Lake Michigan very near the spot selected for one of these stations. Any such discharge has long since ceased, and its exact location has been entirely obscured by the advancing dunes, leaving the remaining river bed as a shallow channel in which the water has little or no current, the present discharge being some eight miles farther west. Dunes are now advancing into this channel at several points, and within a few years will doubtless occupy other portions

of its bed. Here, at a distance of 100 to 200 meters from the shore, the pioneer tree association becomes established, and persists upon dunes of variable size that are usually more or less actively moving. This association is characterized by a paucity of species, all having strongly xerophytic structures. *Populus deltoides*, *Salix glaucophylla*, *S. syrticola*, *Prunus pumila*, and the two grasses *Calamovilfa longifolia* and *Ammophila arenaria* are at this point the only conspicuous members of this rather open cottonwood dune association. In it, upon dunes that have become almost completely fixed, two stations were established on May 6, and a third on July 9, and at the three stations at least four instruments were maintained in constant operation until the last day of October. These stations were about 200 meters from the lake shore, some 100 meters apart, and about 12 meters above the level of the waters of Lake Michigan. At all stations the atmometers received a small amount of shade for a few hours of the day, and on account of the open nature of the association were little sheltered from the wind, the cups receiving a rather sharp sand blast during high winds. Station no. 1 had some sheltering groups of cottonwoods on a slight elevation of sand a few meters southeast of the instruments, and no. 3 possessed a similar but smaller shelter at the southwest. These differences of exposure to winds probably caused some of the variations in the records of the different stations, but affected very slightly the average rate for the season.

The graphs for three cottonwood dune stations have been plotted upon the same chart (fig. 1), and exhibit a great similarity in their general course and in their simultaneous maxima and minima. The rainfall at Chicago (20 miles distant) for the same period, expressed in centimeters, is shown for periods corresponding with those of the intervals between the evaporation readings, but as there seems to be no very exact correspondence between the amount of precipitation and the amount of evaporation, these data are omitted from the other charts. There is certainly a correspondence between the number of hours of cloudy or rainy weather and the amount of evaporation, but this has not been exactly determined, nor does it seem important in our present studies. The evaporation graphs indicate that the most critical period occurs

about the end of July, and this is also toward the end of a period of seven weeks with very little rainfall; hence it may be safe to assume, even without any direct data regarding soil-moisture, that

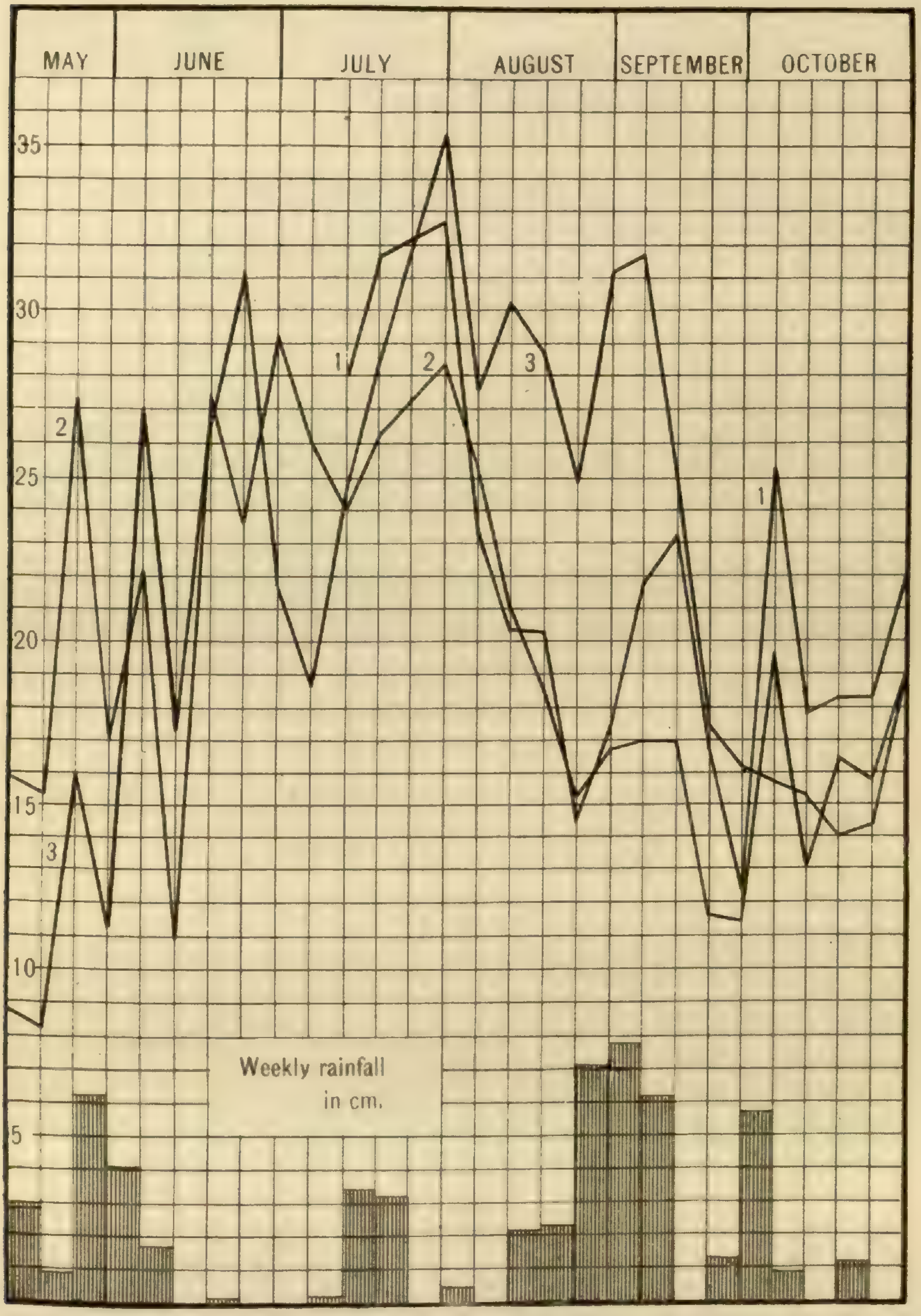


FIG. 1.—Evaporation rates in the cottonwood dune association at stations nos. 1, 2, and 3.

at this time there is a maximum demand by the atmosphere upon the water contained in the plant tissues, while at the same time only a minimum supply is available to replace such losses by transpiration. Two other periods of high evaporation are found to occur, one late in June and the other early in September. The latter is doubtless the one of greater stress, for it follows a month of very low rainfall. It will be seen that the maximum average evaporation for any week is just above 35 cc. per day, and that the minimum only once falls below 10 cc. per day. The average rate for the three stations upon the cottonwood dune for the 178 days of observation is 21.1 cc. per day.

The graphs (fig. 1) indicate that not only is the cottonwood dune an association with a very high rate of evaporation, but also that it is subject to excessive variation. This is most noticeable during May and June, but to a less marked extent prevails through the season, the fluctuations being decidedly greater than in the other associations (fig. 4). The mean of the readings of these three stations is believed to express most accurately the true measure of the evaporating power of the air during the growing season in the cottonwood dune association, and is therefore plotted and used in comparison with similar graphs from the other associations (fig. 4).

As the dunes gradually become fixed, an association dominated by evergreens succeeds the cottonwood dune. This pine dune association varies somewhat in composition in different localities, but in the area under consideration is dominated by *Pinus Banksiana*, associated with *Juniperus virginiana*, *J. communis*, and in the older portions containing also *Pinus Strobus*. In the undergrowth *Arctostaphylos Uva-ursi* is conspicuous, associated with *Rhus canadensis*, *R. toxicodendron*, *Prunus virginiana*, *Celastrus scandens*, seedlings of *Quercus velutina*, *Smilacina stellata*, *Asclepias tuberosa*, *Monarda punctata*, and other woody and herbaceous plants. Two stations were placed in this association at spots of medium density of growth about 100 meters south and east of the cottonwood dune series, but owing to several accidents only one record is worth reporting. This, from station no. 4, is unbroken for 178 days, and is often the mean of the readings from two atmometers.

This association is unique in the dominance of conifers, but is also notable for the comparative abundance of its undergrowth, although many species have decidedly xerophytic characters. That it is a comparatively short-lived association is evident from the presence of seedlings of *Quercus velutina*, the dominant tree of the succeeding association, very early in its history. Comparing the graph of its evaporation with that of the cottonwood dune (fig. 4), it will be seen that it is much lower, never reaching 20 cc. per day, and is subject to less violent fluctuations. Its maxima and minima are nearly synchronous with those of the cottonwood dune. The maximum evaporation rate is 17.5 cc. per day, the minumum falls below 4 cc., and the average for the season of 178 days is 11.3 cc. daily.

Proceeding inland from the lake shore, the pines gradually decrease in numbers, and the black oak, *Quercus velutina*, becomes more plentiful, until at a distance of about 500 meters south of the last station it forms an almost pure stand with only occasional trees of white oak, *Quercus alba*. The shrubby undergrowth consists principally of *Prunus virginiana*, *Rosa blanda*, *Viburnum acerifolium*, *Vaccinium pennsylvanicum*, *Ceanothus americanus*, and seedlings of *Quercus velutina* and *Q. alba*. Among the herbaceous members of the association are *Smilacina stellata*, *Lupinus perennis*, *Tephrosia virginiana*, *Lithospermum canescens*, *Asclepias tuberosa*, *Helianthemum canadense*, *Polygonella articulata*, and *Aster linariifolius*. In this oak dune association four stations were placed within a range of 100 meters; no. 6, on a fixed dune 15 meters high, well covered with the oak forest; no. 7, on a slope at an altitude of about 8 meters; and nos. 8 and 9, on the general floor of the forest some 5 meters above the level of the lake waters. All were about equally exposed and shaded. No. 6 was established on May 6, and the other stations on May 26. Station no. 9 was subject to so many interruptions that no report of its evaporation is presented, but the graphs from the other three (fig. 2) show a very close agreement, with differences corresponding directly to their elevation. A maximum of nearly 19 cc. per day occurred in May during the second week of the record, before the trees were in full foliage. The absence of leaves would largely account for this excessive rate,

but as it occurred when only one instrument was recording, it may be regarded as lacking confirmation, and as it could hardly be a critical period on account of the abundant water supply in the soil, it is disregarded in the general discussion. Throughout the remainder of the season the rate is rather high, but not subject to great fluctuations. A minimum of about 5 cc. per day is reached in September, and is followed by a distinct rise as defoliation pro-

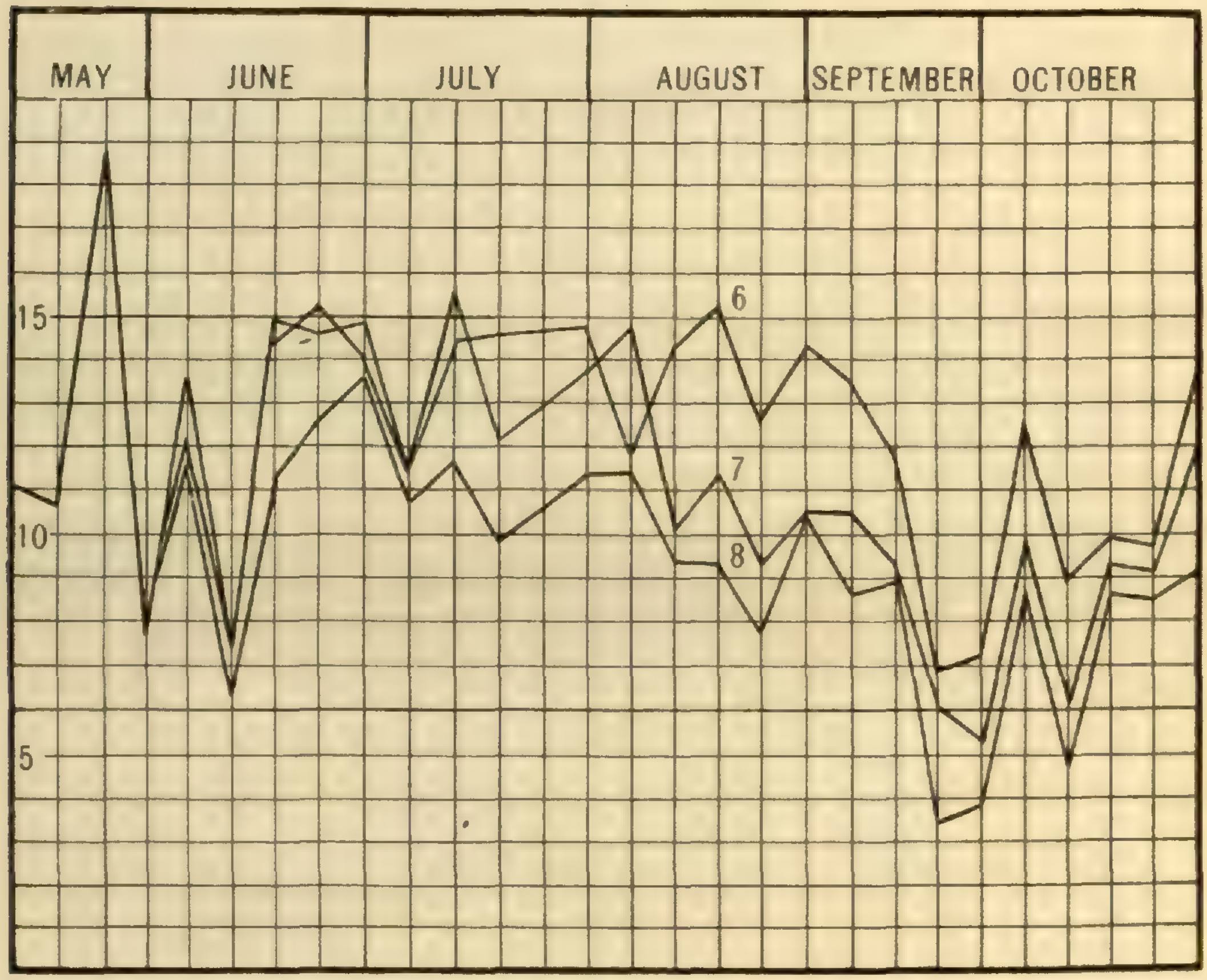


FIG. 2.—Evaporation rates in the oak dune association at stations nos. 6, 7, and 8.

gresses. Station no. 9 (not plotted) gives a somewhat higher rate during July, affording a maximum for that month and for the summer of 16 cc. per day. The average rate for the whole period is 10.3 cc. per day. The mean of all stations in the oak dunes is used (fig. 4) in comparison with similar graphs from the other associations.

At Millers, Ind., the vegetation exhibits no undisturbed successional stages beyond the oak dune, but 15 miles farther east, near the village of Otis, Ind., there is a tract of the climax deciduous

mesophytic forest dominated by the beech, *Fagus grandifolia*, and the maple, *Acer saccharum*. These two species form at least 85 per cent of the tree growth, with the remaining 15 per cent composed of *Tilia americana*, *Ostrya virginiana*, and *Prunus serotina*, and occasional trees of *Quercus rubra*, *Platanus occidentalis*, and *Liriodendron Tulipifera*. The undergrowth is largely seedlings of the dominant tree members of the association, together with *Cornus alternifolia*, *Viburnum pubescens*, *Asimina triloba*, *Sambucus racemosa*, and such herbaceous forms as *Trillium grandiflorum*, *Dicentra*

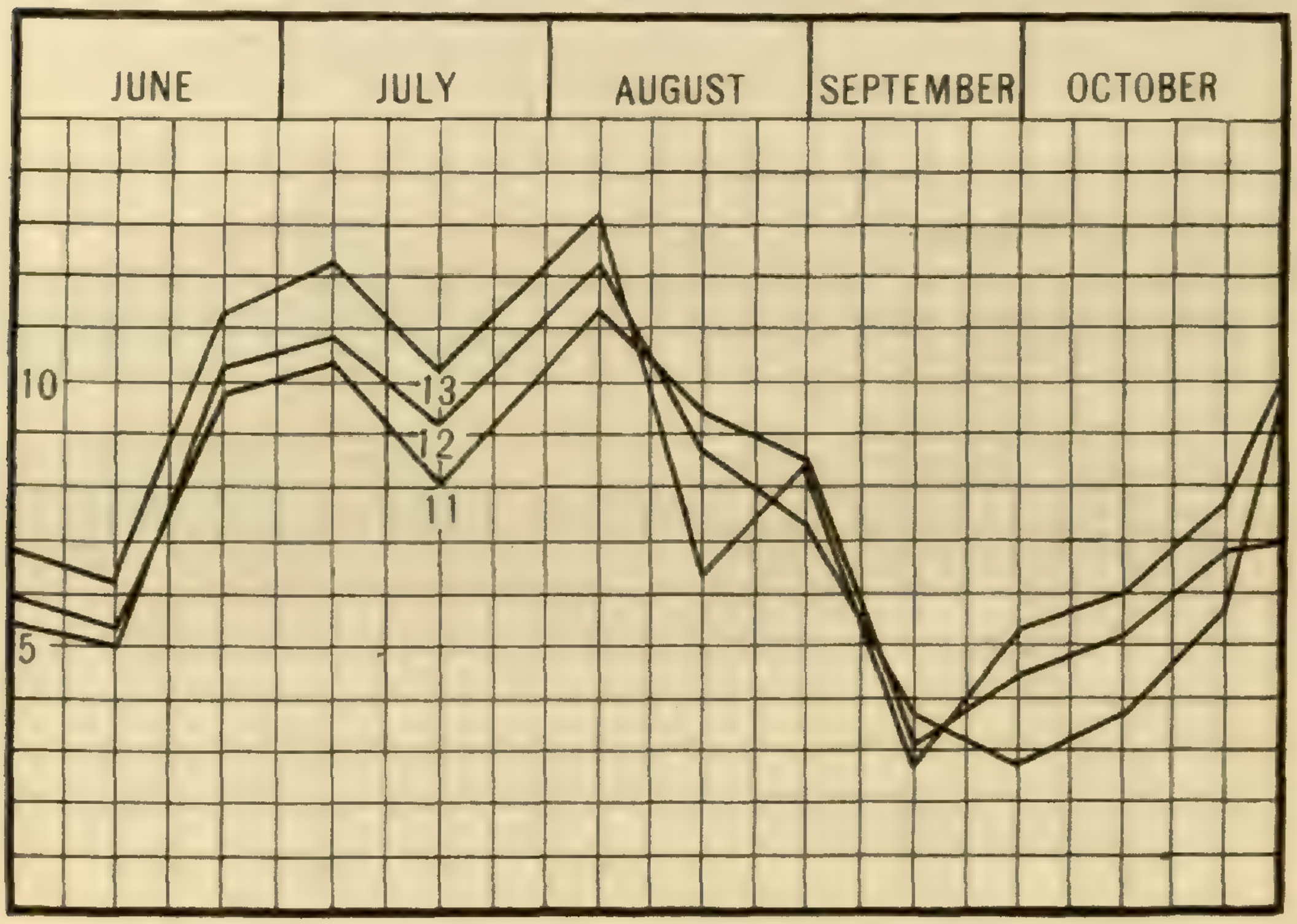


FIG. 3.—Evaporation rates in the beech-maple forest association at stations nos. 11, 12, and 13.

canadensis, *Adiantum pedatum*, *Asplenium angustifolium*, *Polystichum acrostichoides*, *Viola rostrata*, *Impatiens biflora*, *Erigenia bulbosa*, and *Epifagus virginiana*. As this represents the climax formation for a large portion of the United States, it was regarded as a standard to which other plant associations could be referred, and accordingly 3 stations were established in it on May 30, and maintained until the end of October, giving a continuous record for 155 days. On account of the difficulty in reaching these stations, readings were made only every second week throughout

the season. Of the 3 stations in the beech-maple forest, no. 11 was in an area dominated by the sugar maple and well surrounded by maple seedlings. No. 11 was near a large beech tree on a slope covered with *Asplenium angustifolium* and *Impatiens biflora*, while no. 13 was in the midst of beech seedlings between two large trees of the same species. Together they seemed to represent the average conditions in a beech-maple forest. The resulting graphs (fig. 3) are very similar, showing coincident maxima and minima differing but little in amount. The maxima are in July and August, and amount to little more than 12 cc. daily; the minimum occurs in September and is scarcely 3 cc. per day. The average rate of evaporation at the 3 stations for the 155 days is 8.1 cc. per day.

It is here interesting to note the close correspondence between the records for this beech-maple forest and those obtained by TRANSEAU (**8**) in a mesophytic forest containing a small percentage of beech and situated on Long Island, N.Y., where for the period of observation from June 5 to July 2, 1907, the evaporation rate averaged 8.5 cm. daily, compared with 8.4 cm. daily during the month of June, 1910, in the Otis, Ind., forest. While it is not safe to draw any very definite conclusions from records covering but a single month, it may be assumed that the two associations differ very little in the amount of mesophytism developed.

Several methods may be employed in comparing the data obtained from the various evaporation stations. Perhaps the best is to plot upon the same chart graphs representing the mean daily evaporation by weeks, from the several stations in the different associations (fig. 4). It will be seen that the graphs show several similarities, but more differences. The maxima and minima are generally coincident in time and proportionate in amount. All show great irregularity during spring and autumn, and a comparatively high rate during July and August. The general height of the different graphs probably gives the most instructive and interesting differences in the various habitats. That of the cottonwood dune is farthest removed from those of the other associations, and shows a habitat not only with great evaporating power, but one of great extremes, the difference in rate between

two consecutive weeks being nearly or quite 10 cc. per day during May and the first part of June, and on two occasions amounting to an increase of 100 per cent in one week as compared with the preceding. This occurring early during the growing period would doubtless be very unfavorable for the development of any seedlings, especially as it was followed by the very high rates of the succeed-

FIG. 4.—Mean daily evaporation rates in the sand dune plant associations and in the beech-maple forest.

ing months. The high maximum occurring at midsummer would probably prove the excluding factor for all mesophytic plants, even if not combined with such other factors as the deficiency of soil water at the same time. Such a graph seems to depict rather well a habitat of atmospheric extremes making large demands upon all available water, and naturally and necessarily resulting in a xerophytic plant association, with a very limited undergrowth and an almost entire absence of herbaceous plants and seedlings. Perhaps nowhere could an association be found so entirely dependent upon vegetative reproduction for its maintenance, for almost without exception any increase in vegetation is the result of subterranean branches.

The graph for the pine dunes is decidedly lower and more regular in its contour than that of the association which it succeeds. Its four nearly equal maxima would indicate that within its limits there was throughout the summer season a continuous stress rather than a series of violent extremes. On the whole, it shows a water-demand of little more than half of that occurring in the cottonwood dune. Its greatest divergence is plainly due to the evergreen character of its vegetation, and is seen in its low range in May and the first part of June, and again in October, when it falls below that of the oak dunes and is even less than that of the beech-maple forest. This would give good reasons for expecting to find within this association truly mesophytic plants, whose activities are limited to the early spring.

The graph from the oak dune stations shows two surprisingly high points; one during May, that may be partially explained by the absence of foliage; and the other near the end of June, which seems to coincide with maxima in the other associations. On the whole, it is more moderate during the months of summer than that of the pine dune, but the difference is not so great as to make it surprising that its undergrowth differs but little from that found in the pine dune association.

The graph from the beech-maple forest stations is one of moderate height and great regularity. It is but fair to say that weekly readings would probably have introduced some minor irregularities, but without changing its general course or influencing the

average rate for the season. At no point does it reach to half the height of that from the cottonwood dune, but surpasses that of the pine dune in October.

The data of these observations relate only to the stratum of vegetation immediately above the surface of the soil, and would be quite different at a height of one or two meters. This lower stratum, however, is the critical one for a forest association, for the development of tree seedlings occurs within its limits, and

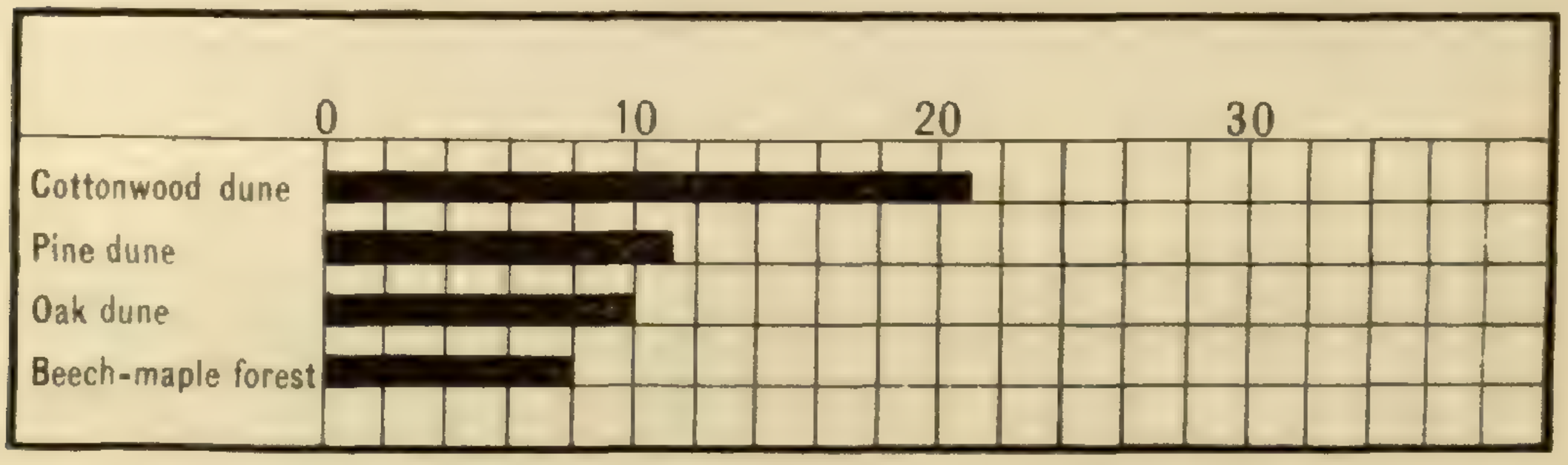


FIG. 5.—Diagram showing the comparative evaporation rates in different associations on the basis of the average daily amount from May 6 to October 31, 1910.

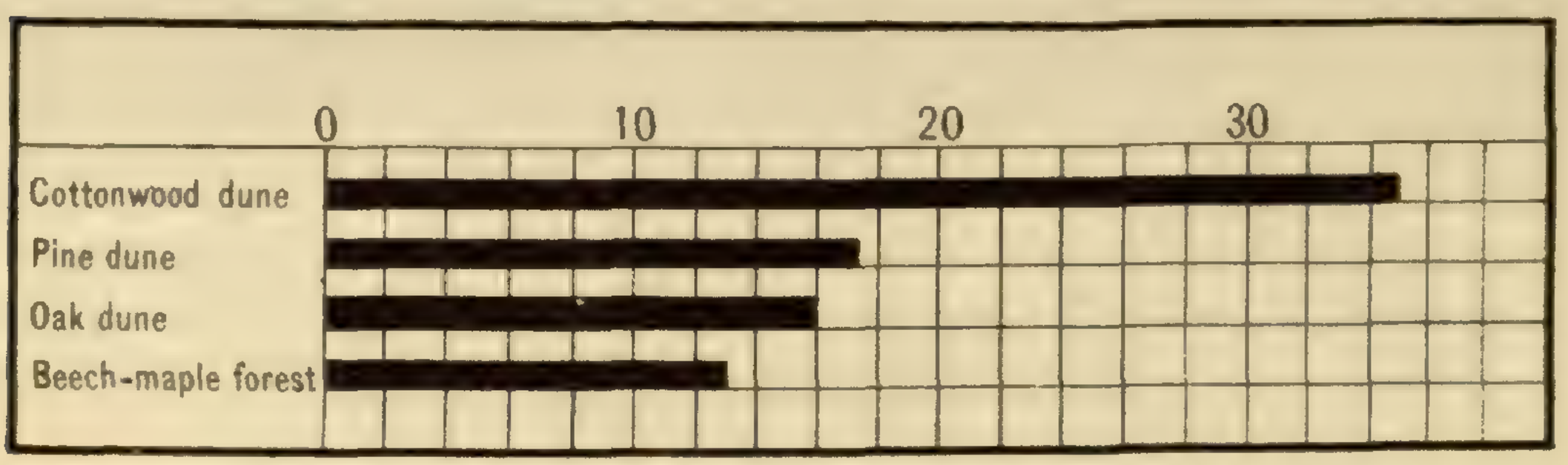


FIG. 6.—Diagram showing the comparative evaporation rates in different plant associations on the basis of the maximum average amount per day for any week between May 6 and October 31, 1910.

therefore it is the portion of the habitat which determines the forest succession and hence the most important ecologically. A single example may be cited from the meager data obtained during the past season regarding the rates of evaporation in the more elevated strata. Very near station no. 13 in the beech-maple forest, an instrument was established 2.5 meters above the surface of the soil, and showed for the season an average of 12.7 cc. daily, as compared with 9.1 cc. daily for no. 13, whose atmometer was 20 cm. above the surface.

The comparative rates of evaporation in the different plant associations may be compared in other ways. If the average amount of water lost by the standard atmometer daily throughout the season be taken as a basis and represented in a diagram giving the loss in cubic centimeters (fig. 5), a graphic representation results which, however, tells little more than what has been shown differently in fig. 4. Likewise, the maximum daily rates for the week of greatest evaporation during the season gives a similar representation of the conditions in the several plant associations (fig. 6). Upon a percentage basis, with the average rate per day throughout the season in the beech-maple forest taken as a unit, the comparative evaporation rate in the oak dune is 127 per cent, in the pine dune 140 per cent, and in the cottonwood dune 260 per cent. As the months of July and August probably represent the critical portion of the growing season with reference to its water supplies, a comparison like the preceding might be made for those months only, when it would be found that the comparative evaporation in the oak dune would be 113 per cent, in the pine dune 146 per cent, and in the cottonwood dune 230 per cent.

Summary

1. These data represent the evaporation rates in the lower but critical stratum of the plant associations.

2. Evaporation at different stations in the same plant association exhibits variations similar in character and degree.

3. The rate of evaporation in the cottonwood dune association, both by its great amount and by its excessive variations, seems a sufficient cause for the xerophytic character of the vegetation and for the absence of undergrowth.

4. Evaporation in the pine dune association exceeds that in the oak and beech associations except when the latter are devoid of foliage.

5. The vernal vegetation of the pine dune is quite as mesophytic as that of the succeeding association, thus agreeing with its lower evaporation rate during that portion of the year.

6. Evaporation in the various associations varies directly with the order of their occurrence in the succession.

7. The differences in the rates of evaporation in the various plant associations studied are sufficient to indicate that the atmospheric conditions are efficient factors in causing succession.

Conclusions

From the study of the data available, it seems evident that the porous-cup atmometer measures with very considerable accuracy the atmospheric factors which combine in making demands upon the water-supply of the aerial portion of the plant; the data, therefore, may be directly related to the plants in an association, and used in determining the comparative xerophytism of plant habitats in so far as they are determined by atmospheric conditions. In such determinations it would appear that the true measure of the limiting atmospheric factors must be found either in the demand throughout the entire growing season as expressed in the average evaporation rate for that period, or in a maximum demand of several days' duration occurring at a period when the water-supply in the soil is deficient, such as would be expressed in a high rate continuing for a week or more in the latter part of the summer. In the associations studied, these demands show practically the same ratio when compared with one another (figs. 5 and 6). If this be the case, we have in the Livingston or Transeau atmometers instruments of sufficient precision to furnish the most valuable quantitative data in the study of plant associations.

A complete study of the water relations of a habitat may be obtained by combining the data supplied by the atmometer with quantitative determinations of the available soil-moisture. It is hoped that some such data may be available in the near future.

It seems highly desirable, in investigations of this character, that the different investigators employ instruments standardized to the common unit recommended by LIVINGSTON (5), and further that a plant association of wide distribution be used as a basis of comparison, and that the conditions in other associations be expressed in terms of these units whenever it is possible to do so. As no association is more widely spread in the United States than the climax mesophytic forest which is frequently characterized by the presence of either *Acer saccharum* or *Fagus grandifolia*, or

both, so no unit seems so well suited for this purpose as the beech-maple forest association or its ecological equivalent. Thus it may be said that the atmospheric conditions in the lower stratum of the cottonwood dune association during the growing season are 260 per cent as severe for plant life as those in the same stratum of the standard association (the beech-maple forest) during the same period.

The writer hopes to continue and extend these investigations during the coming seasons.

Grateful acknowledgment is made of the helpful advice and suggestions of Dr. HENRY C. COWLES, under whose direction this investigation has been conducted.

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THE TETRANUCLEATE EMBRYO SAC OF CLINTONIA

R. Wilson Smith

(WITH PLATE V)

The following results are published in the belief that from the standpoint either of morphology or of phylogeny it is important we should become acquainted with the variations of the angiosperm embryo sac. By searching out and comparing all deviations from the normal type, we may hope to ascertain the directions in which the embryo sac is varying at the present time, and perhaps we may also discover some clue to the path along which it has come. The results here given were obtained from a study of *Clintonia borealis*, collected in the neighborhood of Toronto and of Lake Joseph, Ontario.

The youngest ovaries, collected May 9, showed the ovules already completely anatropous, each with a large archesporial cell, having its nucleus in the synapsis stage (fig. 1). The archesporial cell undergoes no cell division, neither cutting off a parietal cell nor dividing into megaspores, but, as in many liliaceous ovules, passes directely into the embryo sac. Its nucleus, however, suffers a twofold reducing division which is of considerable interest.

The nucleus in the synapsis stage is very large; it is usually situated slightly below the middle of the cell, and occupies fully four-fifths of its width. In the condition represented in fig. 2, the protoplasm is becoming denser about the periphery of the nucleus in preparation for spindle formation, and the loops of chromatic material are beginning to separate and spread throughout the nuclear space. Subsequently, when the fibrils of the spindle are quite distinct, the chromatin is found segmented into chromosomes, which frequently appear in the x's, y's, and other forms, characteristic of the heterotypic division.

The number of these chromosome pairs I have not been able to determine with certainty, since the nucleus is too large to be included in one section. Further, since all my sections are cut

longitudinally to the ovule and therefore at right angles to the equatorial plate, it is difficult to make an accurate count of the chromosomes at a later stage of the mitosis. It is certain, however, that we are here dealing with the haploid number, probably 12. In vegetative divisions 20 or more chromosomes can easily be counted, though in this case also it is not easy to determine the number with certainty. The chromosomes when drawn into the equatorial plate are short and thick, almost globular, strongly contrasting in this respect with the long, crowded chromosomes of the vegetative division.

In none of my material, though careful examination was made, could there be found any difference in the separating chromosomes (fig. 3). Those going to the lower pole are fully as large and give the same staining reaction as those going to the upper pole. But on arriving at the poles of the spindle, the two groups behave very differently. Those at the upper pole unite into a normal nucleus, while those reaching the lower pole fuse together into an irregular lump, without spongioplasm or distinct nuclear membrane. Frequently chromosomes or chromosome fragments fail to reach the principal mass, and remain scattered along the spindle or in the cytoplasm outside. When Flemming's triple stain is used, these fragments, as well as the large chromatic lump, take only the safranin and appear semitransparent, while the chromatin of the upper nucleus, taking the gentian violet, appears dark and opaque. No wall is run in at the close of this division, but a distinct cell plate is formed by the thickening up of the spindle fibers (fig. 4).

Division follows in each of the daughter nuclei resulting from the heterotypic mitosis. My material, however, does not furnish any examples of the prophase of this division, nor any information with respect to the chromosomes. The telophase is represented in figs. 5 and 6. In both figures the remains of the first spindle and its cell plate are still distinguishable (on the left side of fig. 6). A cell plate is formed also on the second spindles, but these and the earlier cell plate are transient structures and disappear shortly.

The division of the upper nucleus results in this case also in the formation of an upper healthy nucleus and a lower irregular lump of chromatin. By the division of the lower of the daughter

nuclei two such lumps are formed. Thus the embryo sac now contains an upper healthy nucleus and three lumps of chromatic material without spongioplasm. The commonest arrangement is that of figs. 6 and 7 rather than fig. 5, the healthy nucleus being somewhat above the middle of the cell and much smaller than the nucleus of the mother cell.

These successive divisions, especially the second, must be completed very rapidly, if one may judge from the rarity of their occurrence in the material. Thus, of about 350 ovules in the stages represented by figs. 2–7, more than 225 were in synapsis, and only 5 in the second division.

It can scarcely be doubted that the four nuclei just described are the four megaspore nuclei, and that megaspore formation in *Clintonia* differs from the normal type simply by omitting the formation of walls and by an earlier beginning of the degeneration of the sterile megaspores.

It is clear that division of the imperfect nucleus formed by the heterotypic mitosis can be of no importance in the subsequent history of the embryo sac; yet among 80 embryo sacs of the age of fig. 7, there was not one in which the lower nucleus had failed to divide. The three sterile nuclei could be found in every case. This fact would imply a strong hereditary tendency to a second division, such as we might expect to accompany megaspore formation; and incidentally it would indicate that the impulse to nuclear division must originate in the cytoplasm, since so imperfect a nucleus cannot be regarded as capable of exercising any of the functions of a normal nucleus.

A second peculiarity of the embryo sac of *Clintonia* is its unipolarity. Only two divisions of the megaspore nucleus occur, and thus are produced four nuclei which, in their position, relation to one another, and later behavior, exhibit the characteristics of the four upper nuclei of a normal embryo sac. The change from megaspore to mature embryo sac, involving two nuclear divisions, requires an interval of about three weeks, and it is therefore difficult to obtain karyokinetic figures. That those I have been able to secure are in the late phases is probably due to slow infiltration of the fixing medium.

The fertile megaspore nucleus moves to a higher position and rests for some time. The spindle of the first division is parallel to the axis of the embryo sac, and the two nuclei formed are always one above the other, as in figs. 8 and 9. Again at this division a temporary cell plate is formed. The second division occurs simultaneously in the two nuclei, and the spindles are at right angles to each other. The two upper sister nuclei and the protoplasm about them become the synergids; of the other two, one surrounded by vacuolated protoplasm and a plasma membrane becomes the egg, and the remaining one is a free nucleus, in position and appearance the upper polar.

Usually at these stages some remains of the sterile nuclei are still recognizable, but it is not always possible to be sure all three are present. They stain much less deeply than when first formed, taking little safranin and appearing to have a dark color of their own, independent of the stain. They vary considerably in size, and very frequently appear pitted or vacuolated, as in fig. 9. They are usually situated in the lower end of the embryo sac, as in figs. 8 and 11; fig. 9 is an exceptional case, since one of the sterile nuclei appears in the micropylar region.

Up to the tetrad stage the protoplasm of the embryo sac shows no tendency to unipolarity; it is coarsely granular and evenly distributed. But after the first division of the megaspore nucleus, when there is considerable enlargement of the sac, the protoplasm of the antipodal region becomes scant and stringy with large irregular vacuoles; that of the micropylar region is much denser, and the numerous vacuoles, which appear only at a late period, are small and globular.

A third peculiarity of *Clintonia* is its comparative sterility. Though it blossoms freely, only a very small proportion of the flowers result in fruit. Propagation by vegetative outgrowths of the rhizome is the common means of multiplication. An examination of 50 ovaries, collected one week after the opening of the flowers, disclosed no embryos and no certain proof that fertilization had occurred. In several embryo sacs one of the synergids was partially disintegrated, and in two cases two free nuclei were found below the egg apparatus, presumably derived from division

of the polar nucleus. Whether or not fertilization occurs normally in those ovaries which develop into fruit, I am at present unable to say, nor can I assign the cause of the large proportion of abortive flowers. Apparently it is not due to any imperfection in the microspore, which contains two normal nuclei and appears plump and healthy.

An attempt to estimate the percentage of fertile flowers by field observation proved futile. An area producing 550 flowers was kept under observation and undisturbed, but all to no purpose. The flowers one and all were abortive, and two weeks after opening had withered and fallen away, leaving only the shriveled pedicels.

An attempt also was made to determine whether the sterility is due to imperfect pollination. A small number of flowers were artificially pollinated, but these like the others yielded no seeds. However, as several days of heavy rain interfered with the experiment, I cannot regard it as conclusive.

Discussion

The interpretation of the embryo sac of *Clintonia* is made easier by recent investigations of certain Onagraceae. GEERTS (**6**) finds that in *Oenothera Lamarckiana* the single archesporial cell gives rise to a tetrad row of megaspores, of which the uppermost develops, slowly absorbing the three lowermost and producing four nuclei arranged much as in *Clintonia*. The same condition is reported by MODILEWSKI (**10**) as occurring in *Epilobium angustifolium*, *E. Dodonaei*, *Oenothera biennis*, and *Circaea lutetiana;* in all these the unipolarity of the embryo sac is strongly marked and there is "double fertilization." A comparison of the embryo sac development of these and of *Clintonia* makes it clear that the four nuclei of figs. 5–7 represent four megaspores. Further, in these six species the unusual condition prevails of having the upper megaspore fertile. The chief differences shown in the development of *Clintonia* are in the absence of walls separating the megaspores and in the large proportion of sterile ovules.

A nearly similar embryo sac occurs in *Oenone* and *Mourera*, two genera of the Podostemaceae examined by WENT (**14**). A mother cell after synapsis divides into two; the upper of these

after division of its nucleus gradually disintegrates; the lower cell also gives rise to two nuclei, one of which, the lower, becomes a mere clump of chromatin, while the other divides twice and the four resulting nuclei arrange themselves as in *Clintonia* and the above named Onagraceae. Though WENT does not discuss the theoretical value of the first four nuclei derived from the mother cell, it seems clear they represent megaspores, of which that next the innermost is the fertile one. Thus two megaspores appear in the upper cell, and two in the lower cell which becomes the embryo sac. The development of one of the middle megaspores, although uncommon, is not unknown. It has been seen in *Acacia* and *Eriobotrya* (GUIGNARD 1881, 1882), *Trapella* (OLIVER 1888), some of the Araliaceae (DUCAMP 1902), and *Asclepias* (FRYE 1902); to this list, which is taken from COULTER and CHAMBERLAIN'S *Angiosperms*, may be added *Vaillantia* and *Collipeltis* (LLOYD 1902).

In the examples thus far reviewed, the four functional nuclei of the embryo sac are the direct derivatives of one of four megaspores. Some cases of a different nature remain for consideration. In *Limnocharis* (HALL 1902) tetrads are not formed; the first two nuclei of the mother cell place themselves at opposite poles, and while the upper gives rise to the egg apparatus and a polar nucleus, the lower remains undivided. Nearly similar is *Helosis*, but in this case the primary antipodal nucleus soon degenerates (CHODAT and BERNARD 1900; I have not been able to consult the original paper). *Cypripedium* (PACE 11) furnishes another example of a tetranucleate embryo sac. In this plant the mother cell divides once and the lower of the two daughter cells becomes the embryo sac, its nucleus undergoing two divisions. Miss PACE interprets the first two nuclei of the embryo sac as megaspore nuclei. Thus according to this view the embryo sac of *Cypripedium* is compound, being the product of two megaspore nuclei.

Miss PACE extended the conception of a compound embryo sac to *Lilium*, in which four megaspores are thought to function, and more recently COULTER (4) has extended it to all those cases in which tetrad formation is apparently suppressed, and especially to the 16-nucleate embryo sac of *Peperomia* and the like.

McALLISTER's (**7**) discovery of temporary walls separating the first four nuclei of the embryo sac of *Smilacina*, which otherwise resembles *Lilium*, is strongly confirmatory of this interpretation. Though the results of the present paper have no direct bearing upon this question, it may be pointed out that in *Clintonia* and the Onagraceae we see for the first time a mature gametophyte of four nuclei proceeding from an indubitable megaspore; and the occurrence in the Penaeaceae (STEPHENS **12**) and *Euphorbia procera* (MODILEWSKI **9**) of four symmetrically placed groups of nuclei, each group similar in appearance to the gametophyte of *Clintonia*, certainly suggests a similar origin for each group. No case is yet known of a 16-nucleate embryo sac derived from one of four megaspores. In *Peperomia* (BROWN **1**) and the Penaeaceae (**12**) there are no tetrads, and reduction occurs in the embryo sac. In *Euphorbia procera* the history has not been traced back to the mother cell. In Gunnera[1] also (MODILEWSKI **8**, ERNST **5**) there are no tetrads. The case of *Pandanus* (CAMPBELL **3**) offers some difficulty; the embryo sac is said to be one of three sporogenous cells (presumably megaspores). But CAMPBELL did not obtain evidence where the reduction divisions occur, and the view that in the group of three "sporogenous cells" the upper two are parietal cells rather than megaspores is a fair inference from his figures and data. The point certainly needs further investigation.

Clintonia, *Eichhornia* (SMITH 1898), *Avena* (CANNON 1900), and *Asperula* (LLOYD 1902) give us examples of four megaspores in one sac, and in *Crucianella* LLOYD (1902) found all four megaspores germinating within the one wall. No one doubts that these are megaspores, simply because three of them or their products disintegrate. But surely the weightier evidence is that of chromosome reduction, and this applies equally to *Lilium*, *Peperomia*, etc. This is the position taken by COULTER (**4**). He maintains that in the genesis of the angiosperm embryo sac "the essential part of the process is found in the first two divisions," and he adds "megaspores, at least their nuclei, cannot be omitted." BROWN (**2**) thinks we cannot make chromosome reduction the sole test of

[1] ERNST understands SCHNEGG (1902) to assert the occurrence of tetrads in *Gunnera Hamiltoni*, but the latter author does not figure tetrads nor use the word, and it seems probable his "Viertheilung" refers to nuclear and not to cell division.

megaspore formation, and he proposes a different criterion. "A distinction," he says, "between the first division of a megaspore and a division giving rise to megaspores is that while in the first case no cell plate is formed on the spindle, in the latter case either a wall or a cell plate is formed on the spindle." BROWN admits the compound nature of the embryo sac of *Lilium* and *Peperomia*, but for the reason just quoted refuses to admit it in the case of *Cypripedium*. To be consistent, he ought not to allow it for *Lilium*, since in this case a cell plate is formed in the third mitosis of the embryo sac. His distinction breaks down, however, in the case of *Clintonia;* in fig. 8 the first division of the megaspore nucleus is accompanied by a cell plate. It seems to the writer that the general principle of a compound embryo sac, while not altogether free from difficulties, furnishes the explanation of a large number of abnormal embryo sacs.

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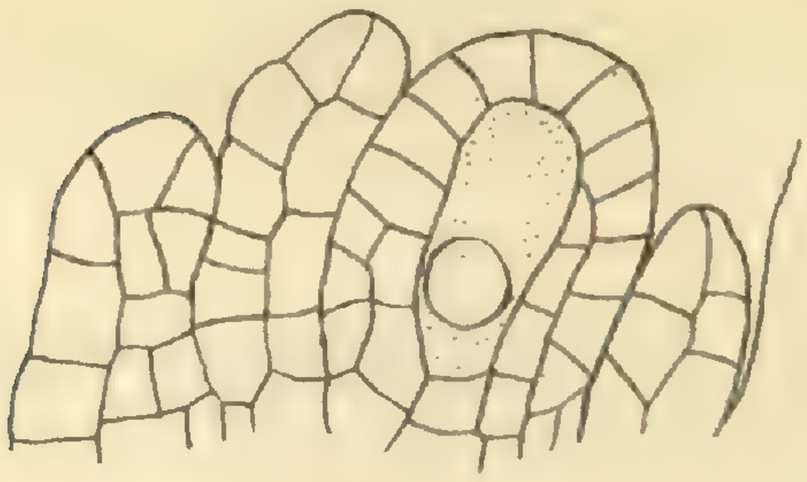

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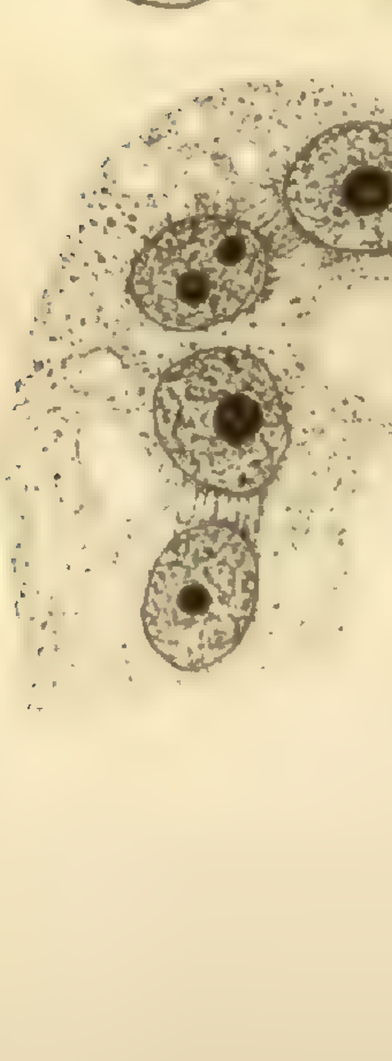

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EXPLANATION OF PLATE V

All the figures were drawn with the aid of an Abbé camera lucida on a Leitz microscope. For fig. 1, ocular 1 and objective 7 were used; for all the others, a 2 mm., 1.30 aper. apochromatic immersion lens with compensation ocular 4. The drawings have been reduced one-half in reproduction.

FIG. 1.—Apex of nucellus with megaspore mother cell.

FIG. 2.—Megaspore mother cell with nucleus emerging from synapsis.

FIGS. 3, 4.—First mitosis in megaspore mother cell.

FIGS. 5, 6.—Second mitosis in megaspore mother cell.

FIG. 7.—Megaspore mother cell with four megaspore nuclei, one healthy and three degenerate.

FIGS. 8, 9.—Embryo sac showing first division of fertile megaspore nucleus.

FIG. 10.—The apex of an older embryo sac.

FIG. 11.—Embryo sac of a fully opened flower; in this, as in all the others, there are no antipodals.

THE EMBRYO SAC OF PHYSOSTEGIA[1]

LESTER W. SHARP

(WITH PLATES VI AND VII)

The material of *Physostegia virginiana* (L.) Benth., upon which the present work is based, was collected near Alma, Michigan, in August 1909. Although the investigation has brought out no new point of fundamental importance, the results are deemed worthy of record.

The ovule arises from the floor of the sporangial chamber as a small protuberance, which in growing pushes out the ovary wall in such a manner that it becomes completely surrounded by the latter except at the funiculus. At the time when the archesporium is distinguishable as a single hypodermal cell, the young ovule is slightly curved, and as growth proceeds this curving becomes more pronounced, until finally an anatropous condition is reached. A single massive integument is developed.

The archesporial cell, which cuts off no parietals, grows rapidly, and is markedly elongated at the time when its nucleus goes into synapsis preceding the first division (fig. 1). This cell, which, on account of the occurrence of the heterotypic prophases in its nucleus, is to be regarded as the megaspore mother cell, by two successive divisions gives rise to a row of four megaspores (fig. 2). Of these the outer three degenerate (fig. 3), while the innermost enlarges and gives rise to the embryo sac.

The nucleus of the functioning megaspore divides, and the two daughter nuclei take up positions near opposite ends of the sac, which becomes strongly curved, and, owing to rapid growth, develops a large central vacuole (fig. 4). Each nucleus divides, forming the four-nucleate stage (fig. 5). These four nuclei by one further division give rise to eight, and walls soon form, resulting in their organization into a typical egg apparatus, three antipodal

[1] Contribution from the Botanical Laboratory of the Johns Hopkins University, No. 20.

cells which soon multiply to several, and two free polar nuclei (fig. 6).

Shortly before the division to form eight nuclei, a laterally directed lobe begins to develop from the antipodal region of the sac, and at the eight-nucleate stage is very conspicuous (fig. 6). It rapidly invades the integumentary tissue, forming what may for convenience be called the "endosperm lobe," since it is soon to contain nearly all of the endosperm formed. During these early stages it probably serves in a haustorial capacity, as does the greatly enlarged antipodal portion of the embryo sac of *Saururus* (JOHNSON 7).

Meanwhile the micropylar polar nucleus migrates to the narrow portion of the sac near the antipodals, where it meets and fuses with the polar nucleus of the antipodal group. The resulting fusion nucleus is invariably found in this position (fig. 7).

At about this time the antipodal cell which lies nearest the sac cavity takes on an appearance different from that of the others. It becomes binucleate, the cytoplasm changes in character, staining more deeply, and rapid enlargement causes its wall to become strongly convex (fig. 7). This enlargement continues until the cell bulges out conspicuously into the embryo sac cavity (fig. 10), and its wall thus partitions off the small pocket in which it lies with the other antipodals. In stages somewhat later it bears much resemblance to the first few cells of the endosperm, but the possibility that it also is of endospermous origin is precluded by the fact that it has been observed side by side with an undoubted endosperm nucleus resulting from the triple fusion (fig. 9).

The function of the cell in question is in all probability haustorial, recalling the behavior of the basal antipodal in several genera of the Galieae (LLOYD 10), although in the sac under consideration the neighboring tissue is not actively invaded. It soon fills all the space formerly occupied by the other antipodals, which disorganize and completely disappear (figs. 13, 14, 16), while in its general form and relation to the vascular supply it is especially well suited to the performance of a nutritive function during the rapid development of the endosperm. Later it disappears and the tissue of the region becomes irregularly broken down (figs. 18–20).

The great variety in form and behavior exhibited by antipodal cells, together with haustorial structures of many types, has been so well summarized (COULTER and CHAMBERLAIN 3) that further comment here is unnecessary, since *Physostegia* offers nothing essentially new.

At the time of fertilization the general aspect of the embryo sac, together with its position in the ovule and its relation to the vascular supply, are as shown in fig. 8. The usual configuration of the egg apparatus is that figured here, but in other cases it exhibits considerable variation from this. In regard to the positions of the nuclei and vacuoles, the synergids represented in fig. 7 show striking similarity to the egg, and it is conceivable that at least the larger one might function as such.

The pollen tube, which has grown down the style into the sporangial chamber, makes its way around the stalk of the ovule, or at times directly over its summit, to the micropyle, through which it enters the embryo sac. Clear cases of fusion of the male nucleus with that of the egg were not observed, but the presence of the pollen tube within the sac, the disorganization of the synergids, the immediate elongation of the egg with divisions to form an embryo, and a triple fusion in the central region of the sac (fig. 9) make it reasonably safe to conclude that fertilization of the usual type occurs.

The formation of the endosperm is of considerable interest. It is initiated by the division of the endosperm nucleus, which occurs in the narrow region of the sac near the haustorial antipodal, as shown in fig. 10. The spindle has a transverse orientation and is very broad, owing to the large number of chromosomes present. The division is accompanied by a longitudinal wall running through the middle of the sac, as shown in fig. 11, which represents a sac cut in a plane at right angles to that of fig. 10. Here the wall is still in process of formation, spindle fibers being evident at its extremities. Extension continues until it comes into contact with the sac wall at or near the end of the endosperm lobe (fig. 12), while in the micropylar lobe it was not observed to do so, and probably ends freely. The nuclei now lying in the two resulting parts of the embryo sac divide, forming transverse

walls (fig. 12), and further similar divisions give rise to a large-celled, thin-walled tissue which fills the endosperm lobe (fig. 13). This endosperm formation may cease abruptly at the narrow portion of the sac (fig. 14), but usually extends for a little distance into the micropylar lobe (fig. 16). The two-ranked arrangement so conspicuous in the endosperm lobe in fig. 13 and in the micropylar lobe in fig. 16 is doubtless due to the longitudinal separation of the embryo sac into two parts as described above.

The cessation of endosperm formation at an indefinite point results in nuclei being left free in the cytoplasm of the micropylar portion of the sac (fig. 13). These nuclei, usually two in number, enlarge (fig. 14) and may occasionally divide, the walls which appear on the spindle fibers being evanescent. Often the nuclei were observed fusing. Consequently, from one to at least four may be present in stages somewhat later, but they play no further active part, and disorganize with the other contents of the micropylar lobe (figs. 18 and 19).

In embryo sacs which show a wall at the first division of the endosperm nucleus it is usual for the sac to be thereby separated transversely into two chambers, and for endosperm to be formed only in the micropylar one. Among such cases the endosperm may pass through a free nuclear stage, as in *Sagittaria* (SCHAFFNER 12), *Limnocharis* (HALL 5), and *Ruppia* (MURBECK 11); or walls may be formed at all of the divisions, as in *Ceratophyllum* (STRASBURGER 13) and the *Nymphaeaceae* (COOK 1 and 2). Less frequently both daughter nuclei resulting from the division of the endosperm nucleus take equal parts in the direct formation of cellular endosperm, as reported for *Peperomia pellucida* (JOHNSON 8), *Heckeria* (JOHNSON 9), and *Datura laevis* (GUIGNARD 4). From the above account it is seen that essentially this is the mode of endosperm formation in *Physostegia*, and in this sac the main point of interest lies in the fact that the first wall is longitudinal rather than transverse. The factors governing the orientation of the spindle and the consequent position of the wall are not at all clear, and the feature is probably best regarded as a minor peculiarity rather than a character of much significance.

The restriction of endosperm to the antipodal portion of the

embryo sac has been observed in a number of cases (COULTER and CHAMBERLAIN 3), the condition reaching its extreme in *Loranthus* (HOFMEISTER 6 and TREUB 14), in which scarcely more than the lower one-tenth of the sac becomes filled with permanent endosperm tissue. Among the Labiatae the work of TULASNE (15), HOFMEISTER (6), and VESQUE (16) shows this to be the prevailing condition in several genera. In *Stachys sylvatica* TULASNE figures endosperm developing in the antipodal region of a slightly curved sac, but without the presence of a special chamber; and in *Betonica* a condition which may well represent a later stage in the same situation. The figures of HOFMEISTER indicate that in *Lamium* the endosperm lobe is well developed before fertilization, as in *Physostegia*. Although no antipodals and only two "Keimbläschen" are represented, HOFMEISTER has figured stages which correspond approximately to those shown in figs. 7, 8, 14, and 16 of this paper.

In all of these cases the embryo is brought into contact with the endosperm by the great elongation of the micropylar cell of the proembryo. The earliest clearly observed stage in *Physostegia* is shown in fig. 13. Here the first division in the fertilized egg has occurred, and the micropylar cell by its great elongation is pushing the chalazal cell into the endosperm, the cells of which at this time are relatively few in number. Nearly all the elongation is accomplished by the one cell, but this soon divides to several (figs. 14 and 16).

The first division in the chalazal cell is longitudinal (fig. 15), as is also the second. Each of the four resulting cells is then divided into two by a transverse wall (fig. 16), and the subsequent divisions proceed with much regularity (figs. 17 and 18).

At the time when the embryo becomes imbedded in the endosperm, the micropylar and endosperm lobes are approximately equal in size. The former, as has been noted above, disorganizes and in later stages becomes entirely obliterated, while the latter increases rapidly in size owing to the active growth of the endosperm. This growth is accomplished at the expense of the cells of the integument, which in the mature seed is recognizable as only one or two layers of cells (figs. 19 and 20). At the same time the

embryo grows rapidly, becomes characteristically dicotyledonous, and displaces nearly all of the endosperm. It attains a length of nearly 2 mm. in the mature seed, the coat of which is formed from the ovary wall.

Summary

1. The archesporium of *Physostegia* consists of a single hypodermal cell, which, without formation of parietals, functions as the megaspore mother cell.

2. The megaspore mother cell by two successive divisions gives rise to a row of four megaspores; the chalazal one enlarges and gives rise to the embryo sac, while the other three disorganize.

3. The mature embryo sac contains an egg, two synergids, three antipodal cells which multiply to several, and two polar nuclei which fuse.

4. During the formation of the embryo sac a lobe develops from near its chalazal end, so that the sac consists of two distinct parts joined by a narrower portion.

5. Double fertilization of the usual type in all probability occurs.

6. The endosperm is cellular from the beginning, the wall accompanying the first division of the endosperm nucleus being longitudinal through the sac. The chalazal portion of the sac, or "endosperm lobe," becomes completely filled with endosperm tissue, which invades and destroys nearly all of the integument; while the micropylar portion of the sac never contains more than a very few endosperm cells, and later disorganizes, becoming completely obliterated by the encroaching endosperm.

7. The first division in the fertilized egg is transverse, and the chalazal cell, which becomes imbedded in the endosperm through the great elongation of the micropylar cell, develops very regularly into a typically dicotyledonous embryo, which displaces nearly all of the endosperm.

This investigation was carried on under the direction of Professor D. S. JOHNSON, to whom the writer is indebted for many helpful criticisms.

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SHARP on PHYSOSTEGIA

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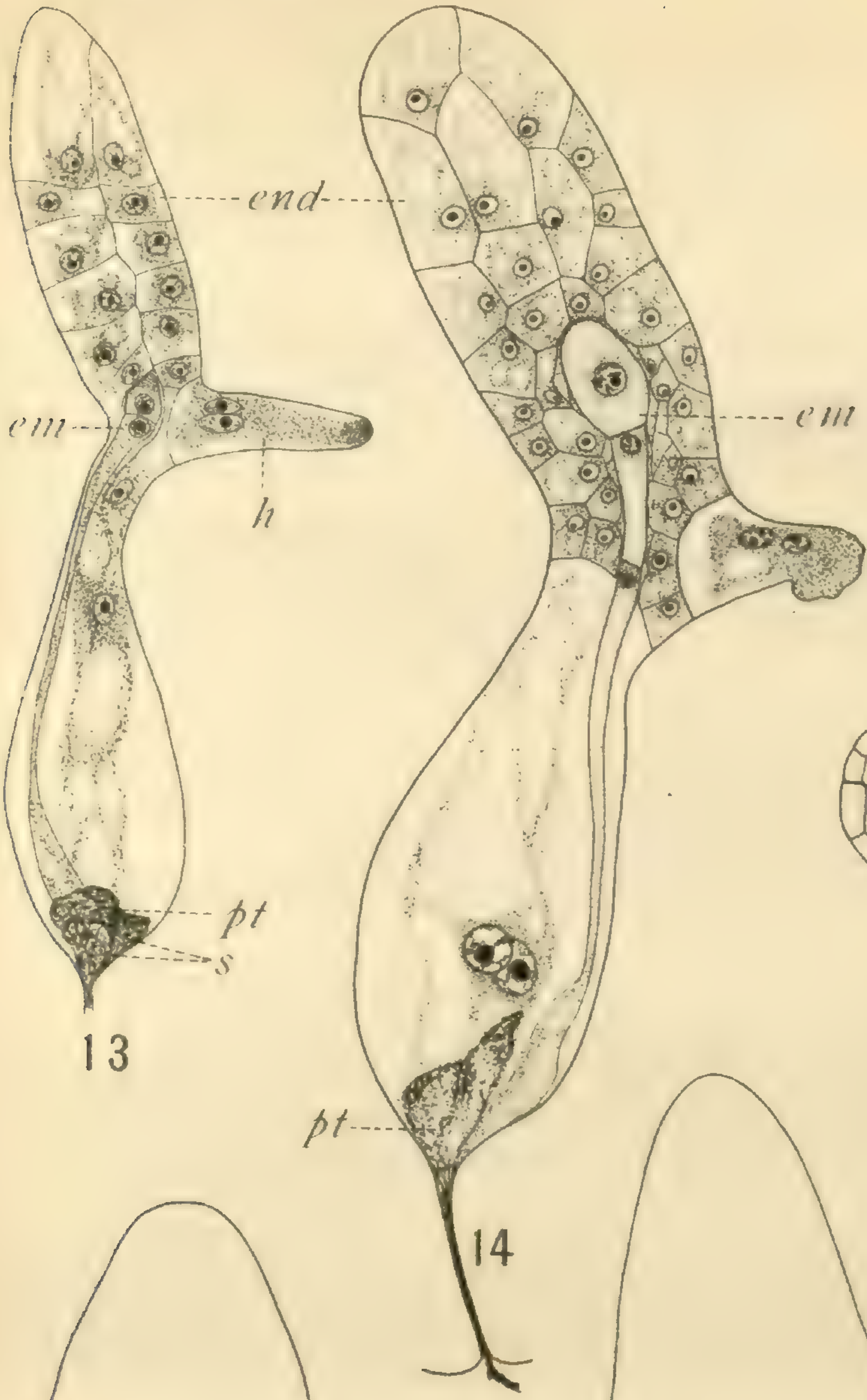

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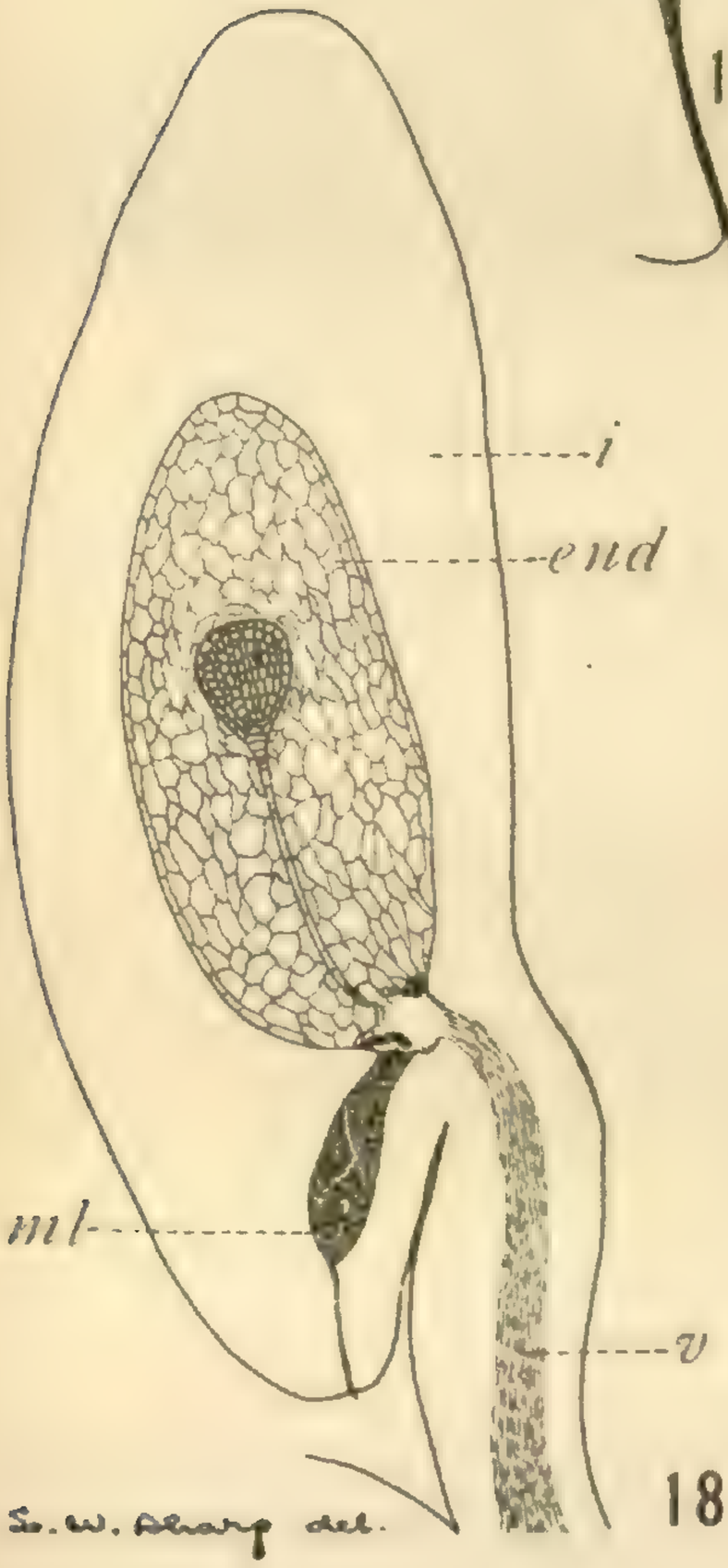

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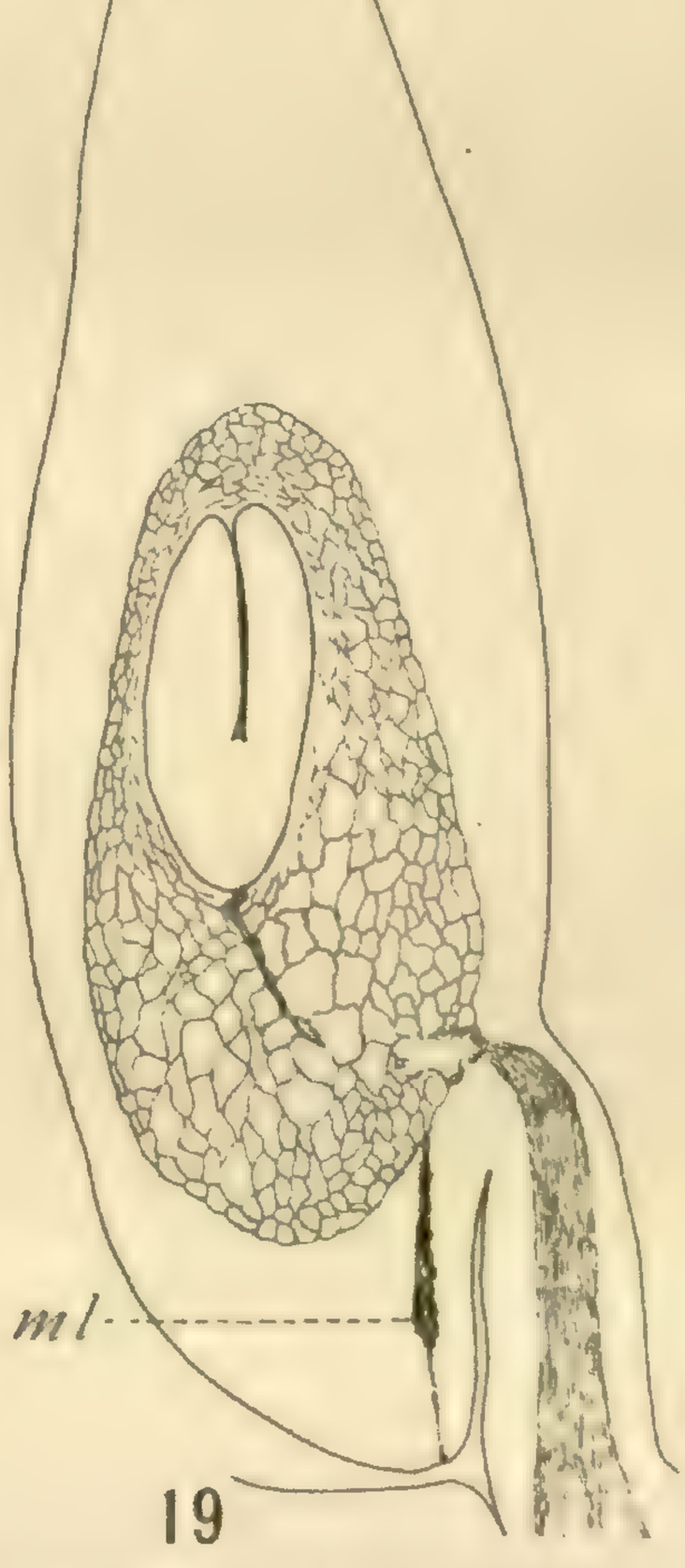

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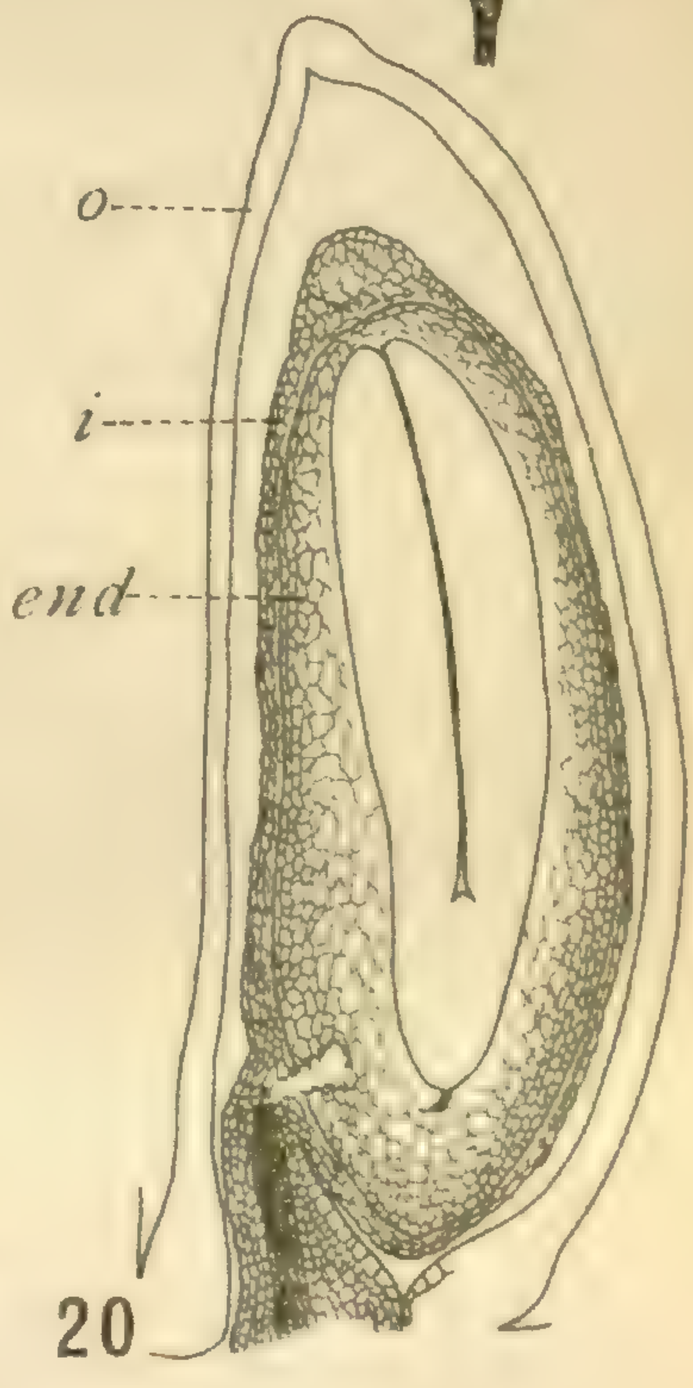

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SHARP on PHYSOSTEGIA

EXPLANATION OF PLATES VI AND VII

All figures were drawn with the aid of an Abbé camera lucida, have a corresponding orientation, and show magnifications as follows: figs. 1, 11, 13–17, ×215; figs. 2–5, 9, ×462; figs. 6, 7, 10, 12, ×385; fig. 8, ×81; figs. 18, 19, ×45; fig. 20, ×25. The following abbreviations are used: *a*, antipodals; *e*, egg; *el*, endosperm lobe; *em*, embryo; *end*, endosperm; *f*, fusion nucleus; *h*, haustorial antipodal; *i*, integument; *ml*, micropylar lobe; *n*, nucellus; *o*, ovary wall; *p*, polar nucleus; *pt*, pollen tube; *s*, synergids; *v*, vascular supply.

PLATE VI

FIG. 1.—Young ovule with archesporial cell nucleus in synapsis.

FIG. 2.—Four megaspores; the division to form the two micropylar ones is delayed.

Fig. 3.—Four megaspores; the innermost one much enlarged, the other three disorganizing.

Fig. 4.—Two-nucleate embryo sac.

FIG. 5.—Four-nucleate embryo sac.

FIG. 6.—Eight-nucleate embryo sac.

FIG. 7.—Mature embryo sac; the polar nuclei have fused and the antipodals have increased in number; one antipodal beginning to differentiate as a haustorial cell.

FIG. 8.—Ovule with mature embryo sac.

FIG. 9.—Triple fusion of male and polar nuclei; haustorial antipodal cell present; other antipodals disorganizing.

FIG. 10—First division of endosperm nucleus.

FIG. 11.—Daughter nuclei resulting from first division of endosperm nucleus; the wall accompanying the division is still in process of formation.

FIG. 12.—Subsequent endosperm divisions, all accompanied by walls.

PLATE VII

FIG. 13.—Two-celled proembryo coming into contact with the endosperm; haustorial antipodal cell well developed; the other antipodals and the synergids have degenerated.

FIG. 14.—Later stage; endosperm formation has ceased abruptly at the narrow portion of the sac in this case.

FIG. 15.—Chalazal cell of proembryo divided longitudinally.

FIG. 16.—Somewhat later stage; the endosperm has extended into the micropylar lobe.

FIG. 17.—Later stage of embryo.

FIG. 18.—Endosperm invading integument; embryo digesting endosperm; haustorial antipodal cell and micropylar lobe disorganized.

FIG. 19.—Later stage.

FIG. 20.—Section of nearly mature seed; the embryo has used up the greater part of the endosperm, which in turn has obliterated nearly all of the integument; seed coat formed from the ovary wall (*o*).

THE BRAZIL NUT[1]

W. J. YOUNG

(WITH PLATE VIII AND ONE FIGURE)

The genus *Bertholletia*, to which is assigned the Brazil nut of commerce, was established in 1808 by HUMBOLDT and BONPLAND, who placed in it a single species, *B. excelsa*. A translation of BONPLAND'S description of the fruit of this species is as follows:[2]

> Fruit a spherical, compound nut the size of a child's head and often larger, divided internally into four cells, each of which encloses several nuts; covered on its exterior with a husk of a green color, smooth and shining.
>
> Main nut very solid, rough and marked by branching furrows on its outer surface, 6 lines (1 cm.) thick, divided internally into four cells by as many membranous dissepiments which become obliterated in part or entirely after the maturity of the fruit, but of which there always remain traces.

The tree is described as 33 m. high, with a trunk 9 dm. in diameter. Leaves alternate, oblong, subcoriaceous, 1 dm. broad and 6 dm. long, borne on short petioles. Type locality, Rio Orinoco.

On account of the great height of the trees, these botanists were unable to obtain the flowers, although it is said that they offered in vain an ounce of gold for specimens.[3] On this account, they were uncertain as to the position which the genus *Bertholletia* should occupy. More recent investigations have established it next to *Lecythis* among Lecythidaceae, an arrangement now universally accepted. It is worthy of note, also, that BONPLAND failed to describe either the operculum or the opercular opening of the fruit, although the latter is shown in his drawing as becoming decidedly narrower at the inner edge.

For more than half a century after the publication of BONPLAND'S description of *B. excelsa*, the genus was accepted as monotypic. Evidence was being gradually accumulated, however, which led to the recognition of a second species. Among the

[1] Published by permission of the Secretary of Agriculture.

[2] BONPLAND in HUMBOLDT and BONPLAND, Plantes equinoxiales 1:110, 111.

[3] SPRUCE, RICHARD, Notes of a botanist on the Amazon and Andes. Edited by A. R. WALLACE. 1:356. 1908.

later botanists to contribute to this end may be mentioned BERG, who in monographing the Brazilian Lecythidaceae described under *B. excelsa* a species distinct from that of HUMBOLDT and BONPLAND.[4] Although BERG'S description is marred by several errors, it is sufficiently accurate to demonstrate that the species described is not the *B. excelsa* of BONPLAND. BERG'S drawing of the fruit or pyxidium is moreover quite different from that of BONPLAND.

It remained, however, for Mr. J. MIERS to point out clearly the distinction between the two plants and to describe BERG'S species under the name *B. nobilis*.[5]

The more noticeable points of distinction between *B. excelsa* and *B. nobilis* are collected from MIERS'S description in the following summary:

B. excelsa Humb. and Bonp.	*B. nobilis* Miers.
Tree 100 ft. or more high, with trunk 2.5–3 ft. in diameter.	Tree somewhat taller than *B. excelsa*, with trunk 14 ft. in diameter.
Leaves green; petioles 9–18 lines long.	Leaves rufescent; petioles 3–6 lines long.
Floral panicle 8 in. long, with single branch nearly equal in length, and nodes $\frac{1}{8}$ in. apart.	Floral panicle 10 in. long, with about 5 short branches, and nodes 0.25–0.5 in. apart.
Fruit slightly elongated, 0.16 in. in length.	Fruit approximately spherical, usually under 5 in. in diameter.
Cortex of fruit smooth, palish, entire, persistent.	Cortex of fruit comparatively thick and rough, darker, cracking as the fruit dries and tending to loosen and drop off as the fruit is handled.
Opercular opening with straight or concave walls, narrowing slightly at its inner edge.	Opercular opening with sharp edge and concave walls, and widening considerably inward.
Operculum cylindrical, with roundish, indented apex.	Operculum oval or radially compressed, conical and pointed at the apex.
Operculum breaks away and falls from the fruit as the columella shrivels.	Operculum remains attached to remnant of columella and, as the latter shrivels, falls into the cavity of the fruit.

[4] BERG in MARTIUS' Flora Braziliensis, I. **14**:478.

[5] MIERS, J., On the Lecythidaceae, *Bertholletia*. Trans. Linn. Soc. II. **30**:195–199.

The differences noted above, as far as they relate to the fruit, are well shown in the copy of MIERS's drawing, reproduced half-size in text fig. 1.

The idea that *B. excelsa* Humb. and Bonp. is the source of commercial Brazil nuts has become so thoroughly grounded in popular and even in botanical literature that it seems to be accepted on faith and passes unchallenged. The extent of this belief will be apparent when we consider that of the following quotations only the last two, or possibly three, make any mention of a second species, to which, moreover, they assign a wholly subordinate position.

Brazil nut.—One of the triangular edible seeds of a tall South American tre (*Bertholletia excelsa*).—Standard Twentieth Century Dictionary.

Brazil nut.—The seed of the fruit of *Bertholletia excelsa.*—Century Dictionary.

Brazil nut.—An oily 3-angled nut, the seed of the lecythidaceous Brazilian tree *Bertholletia excelsa.*—Webster's New International Dictionary.

Cream nut (*Bertholletia excelsa* Humb. and Bonp.).—This is a common nut in our markets brought from Brazil; hence it is often called Brazil nut.—Nut culture in the U.S., p. 106, Div. of Pomology, U.S. Dept. Agriculture

Brazil nuts, cream nuts, Para nuts.—These are edible nuts imported from Brazil. The nuts are the product of *Bertholletia excelsa* (Humboldt and Bonpland).—U.S. Disp., 19th ed., p. 1420.

Bertholletia excelsa.—Brazil nut.—A large tree belonging to the family Lecythidaceae, and yielding the Brazil or Para nuts of commerce. A tree 100 to 150 ft. high, distributed throughout northeastern South America to the Island of Trinidad.—COOK and COLLINS, Economic plants of Porto Rico, Contrib. U.S. Nat. Herb. **8**:91. 1903.

Berholletia Humb. and Bonp.—Tall trees. One or two species. South America.

a. B. excelsa Humb. and Bonp.—*Seeds*, Brazil nuts, Para nuts, cream nuts, nigger toes, Castana nuts.—LYONS, A. B., Pl. names, sci. and pop., 2d ed., p. 71.

Bertholletia.—Brazil nut, Para nut, cream nut, nigger toe.—Species 2, both of which furnish Brazil nuts.—HASTINGS, G. T., in BAILEY'S Cycl. of Hort.

The Brazil nut, also called Para nut, from the port of shipment, is the seed of a large tree (*Bertholletia excelsa* Humb. and Bpl.).—Another species, *B. nobilis* Miers, also yields a similar nut.—WINTON, A. L., Microscopy of vegetable foods, p. 312.

This state of affairs seems to be due primarily to BONPLAND'S assumption, stated in connection with his description of *B. excelsa*,

that it is this species which furnishes the Brazil nut. The long time which elapsed previous to the identification of a second species allowed this view to become so thoroughly established that MIERS's work appears to have been overlooked by persons inter-

FIG. 1.—Reproduction of MIERS's drawings of *Bertholletia*, copied half-size from Trans. Linn. Soc. **30**: *pl. 37. figs. 1–3, Bertholletia excelsa: 1*, pyxidium cut open to show structure; *2*, section of opercular opening; *3*, operculum; *4–7*, *Bertholletia nobilis: 4*, pyxidium cut open to show structure; *5*, section of opercular opening; *6*, operculum; *7*, a cluster of seeds (Brazil nuts).—Published by courtesy of the Linnean Society of London.

ested in botany from the economic standpoint. The work of various botanists during this interval, and especially BERG'S description of *B. nobilis* under the name *B. excelsa*, no doubt contributed to the same end. Moreover, the seeds of the two species, so far as can be judged from the descriptions and drawings available, are so similar as to be distinguished with difficulty if at all.

After making a careful study of the situation, the writer has become convinced that the commonly accepted view is erroneous, and that the Brazil nuts of commerce are derived from *B. nobilis* Miers (*B. excelsa* Berg) and not from *B. excelsa* Humb. and Bonp. The reasons for this view are given below.

1. Commercial samples of Brazil nuts contain, in larger or smaller numbers, opercula derived from the fruit, and the presence of these in itself is evidence that the nuts were derived from *B. nobilis*, since, as has been noted in the comparison, the opercula fall from the mature pyxidia of *B. excelsa*, and hence would not find their way into samples of nuts from that source. On the other hand, their presence among nuts from *B. nobilis* is perfectly normal and what would be expected, since in this species the opercula fall into the interior of the pyxidia and become mixed with the nuts. Moreover, the opercula, so far as the writer has been able to observe, are always of the *B. nobilis* type, as shown in fig. 1. They vary in form from ovoidal bodies to cones of varying slope, being modified apparently by the size and degree of persistence of the columella, as well as by the extent of the grinding against surrounding nuts to which they have been subjected during shipment. All, however, are provided with a distinct apical point except where it has been broken off, in which case the fact is usually quite evident. It cannot be denied that the absence of opercula of the *B. excelsa* type does not preclude the possibility that nuts of this species may be occasionally mixed with those of *B. nobilis*, since the writer is not aware that it is possible to distinguish the species from the character of the nuts alone.

2. Every pyxidium of the Brazil nut which the writer has had an opportunity to examine has indicated that the fruit is that of *B. nobilis*. Their main points of structure are well shown in

1

2

3

YOUNG on BRAZIL NUT

figs. 2 and 3, which illustrate pyxidia obtained from different sources. A comparison of the photograph with MIERS's description of *B. nobilis* will leave no doubt of their identity. Most if not all of the pyxidia which the writer has examined were brought to this country by the importers of Brazil nuts, and represent the source of the nuts in which they deal.

3. The testimony of others, although comparatively scanty, should not be overlooked, since it is improbable that the authorities quoted as stating that the Brazil nut is the seed of *B. excelsa* have given the matter any exhaustive study. After this description of *B. nobilis*, MIERS states "these seeds are known in commerce as Brazil nuts," and proceeds to give statistics regarding their exportation and use. Moreover, BERG'S error regarding *B. excelsa*, although perhaps adding to the confusion, is in reality indirect evidence of the same fact, since it is doubtful whether he would have confused the two species had he not been sure that the specimens from which he made his description were those of the Brazil nut, which he, in common with others of his time, regarded as *B. excelsa*.

NOTE.—Acknowledgment is due Mr. H. C. SKEELS of the Office of Foreign Seed and Plant Introduction, U.S. Dept. of Agriculture, who has reviewed the work and confirmed the conclusions of the writer.

U.S. DEPT. OF AGRICULTURE
WASHINGTON, D.C.

EXPLANATION OF PLATE VIII

Bertholletia nobilis Miers.—The form of the operculum and opercular opening, and the loose, broken cortex are characteristic of this species.

FIG. 1.—Opercula from commercial Brazil nuts; $\times\frac{2}{3}$.

FIG. 2.—Entire pyxidia; $\times\frac{3}{8}$.

FIG. 3.—Pyxidium cut open to show structure; nuts in place; small specimen; natural size.

BRIEFER ARTICLES

AN IMBEDDING MEDIUM FOR BRITTLE OR WOODY TISSUES

A mixture of rubber and paraffin as an imbedding medium for brittle objects was first described by J. B. JOHNSTON,[1] and the following is a modification of his original formula.

Melt 98 grams of paraffin of the melting point usually used, to it add 0.4 gram of asphalt (mineral rubber) and heat until the asphalt is dissolved, giving the paraffin a dark color. The purpose of the asphalt is to increase the power of the paraffin to dissolve rubber. For very woody tissue so much asphalt may be added that the paraffin becomes black. To the dark-colored liquid paraffin add 2 grams of crude rubber cut into very small pieces, and keep the mixture at a temperature of 95° C. for several hours, or at the melting point of the paraffin for several days until the solution is saturated with rubber. Then decant the clear supernatant liquid and allow it to cool. Use the dark solid exactly as paraffin is used.

There are two points which require care in manipulation. First, as the rubber tends to separate out slowly if the mixture remains in the melted condition too long, allow the mixture to cool when not infiltrating; second, the elasticity of the mixture leads to the formation of internal air bubbles if the "blocks" containing the imbedded object are cooled too rapidly. During winter, when the water is very cold, it is best not to immerse the blocks completely, but simply let them rest on the surface until hard. The addition of the rubber decreases the melting point of the mixture by two or three degrees.

The relative amounts of the different components of the mixture can be modified to suit individual requirements, and with a little practice the results obtained equal those obtained with the much more cumbersome celloidin method.—H. M. BENEDICT, *University of Cincinnati.*

[1] Journ. Micr. and Lab. Methods **6**: 2662. 1903.

CURRENT LITERATURE

BOOK REVIEWS

Plant and animal breeding for secondary schools

There has been a growing demand in recent years that the secondary schools, especially those located in rural districts, shall give courses in agriculture, domestic economy, and other subjects bearing a practical relation to the life of the people in whose midst the schools are located. In several states these subjects are now a part of the prescribed course. Such requirements make demands for properly trained teachers and for suitable text-books. A well-conceived and charmingly written manual of plant and animal breeding has been prepared by Professor EUGENE DAVENPORT[1] to partially meet this growing need.

In some respects this work is essentially an abridgment of the same author's earlier work on *Principles of breeding*, but less attention is given to philosophical discussions and more to facts regarding the origin and history of the various domesticated races. Several early chapters describe the manner in which plants and animals came to be domesticated, and point out the need of their further improvement. A chapter on the "ways of the wild" gives a very readable discussion of natural selection and the survival of the fittest, thus giving a basis for a proper appreciation of the relation between artificial selection and the natural evolutionary processes. The principles which are involved in the improvement of plants and animals are then discussed at some length, chief attention being given to GALTON'S *Law of ancestral heredity* and the correlation table.

MENDEL'S laws are given very inadequate treatment. The author evidently has hazy conceptions of unit characters, dominance and recessiveness, latency, atavism, mutation, etc., and his discussions involving these subjects lack the definiteness and accuracy which characterize the rest of the book. He repeatedly emphasizes the statement that each individual possesses all the characteristics of all its ancestors, a statement directly opposed to all Mendelian experience. This lack of precision in the treatment of the principles of Mendelian heredity constitutes the most fundamental defect of the book. It is not only too plainly apparent in the discussions, but is also seen in a number of erroneous definitions in the glossary, as the following examples plainly show: "Gamete, the fertilized ovum"; "Mutant, an individual or

[1] DAVENPORT, E., Domesticated animals and plants. A brief treatise upon the origin and development of domesticated races, with special reference to the methods of improvement. pp. xiv+321. *figs.* 49 and frontispiece. Boston: Ginn & Co. 1910.

strain essentially new and produced spontaneously by nature through crossing, bud variation, or otherwise, synonymous with the older term 'sport'"; "Zygote, that portion of the gamete which determines a unit character." It seems unfortunate that a book otherwise so admirable should propagate such definitions as these. However, the defect in regard to Mendelian heredity is mainly a "sin of omission," and the prepared teacher can easily fill in the vacancy, especially with the aid of PUNNETT'S *Mendelism*. DAVENPORT'S book can not fail to interest, instruct, and inspire, and is deserving of a wide distribution.—GEO. H. SHULL.

Popular manuals

The scientific men and women of England have always been interested in interpreting the result of science to the intelligent public not trained in science. Even their scientific papers are apt to be more popular in form than are those prepared in the United States. We cannot but feel that science in America has suffered very much from lack of proper interpretation. Those who are willing to write on scientific subjects for popular reading are usually unfit for the task; and those who are fit, are unwilling. The projected *Cambridge Manuals of Science and Literature* furnish a notable illustration of the continuous effort in England to interest the public in scientific matters. They are not intended primarily "for school use or for young beginners," but also for educated readers who want brief and simple, and at the same time authoritative statements of recent discoveries. The five volumes now issued, dealing with science, will indicate the subjects treated and the kind of authors preparing them.

The coming of evolution, the story of a great revolution in science, by JOHN W. JUDD (171 pp.); *Heredity*, in the light of recent research, by L. DONCASTER (140 pp.); *Plant-animals*, a study in symbiosis, by FREDERICK KEEBLE (163 pp.); *The natural history of coal*, by E. A. NEWELL ARBER (163 pp.); *Plant life on land*, considered in some of its biological aspects, by F. C. BOWER (172 pp.).

To issue such a series, at one shilling a volume, is to place this material in the hands of a very wide range of readers, and must react favorably upon the general interest in science.

Another series, having the same purpose, is called *Home University Library*, ten volumes of which have now appeared. It is an English series (Williams and Norgate), as one might expect, published in this country by Henry Holt and Company. The books are larger than the Cambridge Manuals (uniformly 256 pp.), selling for 75 cents, and are more pretentious in contents, suited doubtless to a somewhat better trained group of readers. Four of the volumes are of interest to botanists, as follows: *Modern geography*, by MARION I. NEWBIGIN; *Polar exploration*, by W. S. BRUCE; *The evolution of plants*, by D. H. SCOTT; *Evolution*, by PATRICK GEDDES and J. ARTHUR THOMSON.

A third series is the *Appleton's Scientific Primers*, edited by J. REYNOLDS GREEN, an English botanist. Three of this series have appeared, the third by the editor and entitled *Botany*. It is written from the English point of view, which lays much stress on details and terminology, but is effective in presenting the plant as a living organism, for the author is a physiologist. A great deal of material is packed in the 128 pages, and it would be interesting to know the impression such material makes upon those without laboratory experience.—J. M. C.

Mendelism

PUNNETT's little book[2] on Mendelism, which was one of the first attempts at a simple popular presentation of its subject, has been completely rewritten and enlarged for its third edition. It is in fact a new book, written however from the same point of view and for the same circle of readers. The author limits himself to the presentation of illustrative examples, with no attempt at exhaustiveness in any phase of the subject, referring readers to BATESON'S book on *Mendel's principles of heredity* for more detailed information and for references to the literature. The material used to illustrate the various principles is well chosen, and is mostly derived, as might be expected, from the work of the Cambridge group of geneticists, of which the author is one. This results in a decided advantage, since the author's familiarity with his material favors clarity and vividness of presentation. The slight sense of provincialism given by this method is in this way more than compensated for.

While the treatment is in the main admirable, several unfortunate errors have crept in. It is stated (p. 2) that "among animals the female contributes the ovum and the male the spermatozoon; among plants the corresponding cells are the ovules and pollen grains." Several other zoological writers on genetic subjects have obviously made the same mistake. The animal ovum (after maturation) and spermatozoon are homologous cells, but ovules and pollen grains are not single cells, and not even homologous structures, the ovule consisting mostly of maternal somatic tissue, and the pollen grain being a much reduced gametophyte. The embryo sac within the ovule, and the sperm nuclei in the pollen tube, approximately correspond to the ovum and spermatozoa. On page 51, line 16, *c* should be *C*, and in fig. 8 on the following page the three squares which are black should be albino, and the three marked "albino," but containing *C*, should be black. The author assumes that dominance of a character always indicates that such character is due to something added to the recessive form, thus ignoring the possibility pointed out several years ago by the reviewer[3] that the positive character may be reces-

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[2] PUNNETT, R. C., Mendelism. Third edition, entirely rewritten and much enlarged. pp. xiv+192. *pls. 6* and frontispiece. *figs. 32*. New York: The Macmillan Co. 1911.

[3] The "presence and absence" hypothesis. Amer. Nat. **43**:410–419. 1909.

sive through the failure of the unpaired gene in the heterozygotes to produce a visible effect.

A number of excellent text figures and six plates, five of them colored, add greatly to the attractiveness of the book, and the press work leaves nothing to be desired.

This little manual is worthy of an even larger measure of the appreciation which has been given to its two preceding editions by those engaged in other scientific fields, and by general readers who are not themselves engaged in science, but who like to keep themselves informed on the advances that are being made in science.—GEO. H. SHULL.

MINOR NOTICES

Alpine plant life.—In an attractive volume intended for the general reader, ARBER[4] has described the plant life of the higher altitudes of the Swiss Alps. The plants are treated in ecological groups, and an evident effort has been made, not unsuccessfully, to maintain the ecological point of view throughout. It might be questioned if most modern ecologists would find as many beautiful adaptations as are evident to the author, who declares that not only the color of the flowers, but the density of their pigment "may be primarily due to a specialization in favor of a particular class of insect visitor." Other adaptations of alpine plants receive considerable attention, and the probable origin of the alpine flora is briefly discussed.

The text is pleasing in style, the descriptions are accurate and profusely illustrated by more than 75 excellent plates and figures. A glossary of botanical terms and a chapter on the structure of the flower should make all the descriptions intelligible even to the reader who is entirely without scientific training.—GEO. D. FULLER.

NOTES FOR STUDENTS

Cecidology.—The anatomy and histology of insect galls continues to be an interesting and profitable field not only for the entomologist, but also for the plant pathologist and the experimental biologist. WEIDEL[5] gives us a valuable study of the life history of the gall of *Neuroterus vesicator* Schlecht. He first calls attention to the failure thus far to explain experimentally the reason for gall formation, and the necessity of comparing the structure of the gall with the normal structure of the plant. After briefly reviewing the history of the study of the gall structures, especially the studies of BEYERICK, who attributed the gall characters which are recognized by the zoologist to a "growth enzyme," he discusses his methods. These methods are well worthy

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[4] ARBER, E. A. NEWELL, Plant life in alpine Switzerland. 8vo. pp. xxiv+355. *pls. 47. figs. 30.* London: John Murray. 1910. $1.50.

[5] WEIDEL, F., Beiträge zur Entwicklungsgeschichte und vergleichenden Anatomie der Cynipidengallen der Eiche. Flora **102**: 279–334. *pl. 15. figs. 49.* 1911.

of notice by our American workers. The mature galls were taken into the laboratory and the insects hatched. These insects were then imprisoned in glass cylinders with leaves and buds of the oak, and the oviposition observed. The material was then fixed in Flemming's fixer at various intervals following oviposition, and sectioned. He confirms the observations of BEYERICK on the ovipositions, and states that in this species the female does not puncture the plant tissue. The "growth enzyme" is from the larva, and the gall formation begins with the hatching of the larva, which becomes inclosed by a cell growth within about 24 hours. In the second part of this paper the author makes a comparative study of the sclerenchyma cells of a number of galls. He also states that the character depends somewhat upon the part of the host plant on which the gall is formed.

KÜSTER[6] gives a brief discussion and criticism of one of TROTTER'S[7] recent papers, in which he compares the protoplasmic and histological characters of certain galls with the primary axis of the dicotyledonous plants. He agrees in part, and cites the great similarity between galls and fruits as evidence. He calls attention to the necessity of comparative study of the structure of gall with the normal structure of the plant. The galls and dicot stems both have the radial arrangement of parts, with parenchyma tissue in the center, but the fibrovascular bundles of the galls are not so well developed as in the stems. KÜSTER sees enough differences in structural characters to prevent agreement with TROTTER, but does not go into an extended discussion of these differences.

GREVILLIUS[8] gives a very interesting discussion of certain pseudo-galls or Thysanopterocecidia. The first of these was briefly described by RUBSAAMEN in 1901. The author agrees with RUBSAAMEN, but gives a more detailed discussion. The insect attacks the upper surface of the leaf, causing the tips to curl. The upper epidermis is seriously injured and the mesophyll somewhat distorted, but the palisade cells only slightly changed. The mesophyll is poorer in chlorophyll than in the normal leaves. When the buds are attacked they fail to develop. A similar gall not previously described occurs on *S. graminea*. A Thysanopterocecidia on the *Polygonum Convolvulus* is also described, but in this the insect attacks the under surface of the leaves. The structural characters are practically the same as the preceeding.

The LEEUWEN-REIJNVAANS[9] give a fourth paper on the cecidia of Java,

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[6] KÜSTER, ERNEST, Ueber die Sprossähnlichkeit der protoplasmatischen Gallen. Marcellia **9**:159, 160. 1911.

[7] TROTTER, A., Sulla possibilita di una omolgia caulinare nelle galle prosplastiche. Marcellia **9**:109. 1911.

[8] GREVILLIUS, DR. A. Y. VON, Notizen ueber Thysonopterocecidien auf *Stellaria media* Cyr., *S. graminea* L., und *Polygonum Convolvulus* L. Marcellia **9**:161–167. 1910.

[9] LEEUWEN-REIJNVAAN, J. und W. DOCTORS, Einige Gallen aus Java. Vierter Beitrag. Marcellia **9**:168–193. 1911.

in which they describe 50 specimens, most of which are caused by insects of the genus *Cecidomyia*. This material was collected in the Oengaran mountains at an elevation of 700 to 1000 meters. Large, soft galls with water parenchyma were especially abundant.

TROTTER[10] gives brief descriptions of 24 species of galls collected by Dr. FORTI in Asia Minor, and occurring on *Quercus aegilops* L. (*Q. vallonea Kosch.*), *Q. lusitanica* Lan., and *Rosa* sp. Most of these species had already been described.

KIEFFER (Bitsch) and HERBST (Valparaiso)[11] describe seven new species of cecidia and insects producing them, from Chile, and give brief descriptions of those species not previously described.

Among the papers on American cecidology we note FELT'S[12] key, parts of which will be serviceable to the botanist as well as to the entomologist, but there are not enough characters of the galls given to enable exact determinations.

EDITH M. PATCH[13] gives a most excellent piece of work on the aphis galls of the elms. Although, with the exception of brief descriptions of the galls, the major part of the work is devoted to the biology and life history of the insects, the work is of great value to the botanist. Several species which have previously been very much confused are separated in a manner which makes them easily distinguishable. The value of the work is increased by the illustrations and bibliographies.

SMITH'S[14] bulletin comes to us as a valuable contribution on bacteriocecidia. The historical discussion and the long series of experiments are interesting and valuable. It is very doubtful if any cecidia have a wider range of host plants than has been proven for this one. The fact that the galls are produced most readily in soft, rapidly growing tissues, is in harmony with results already obtained by the study of insect cecidia, and further studies will doubtless bring out other similarities. The very limited discussion given to the stimulus and to the character of the cecidia leads us to hope for another bulletin in which these phases of the subject will receive more attention.

NORTON[15] records a very interesting crown swelling of the peach due to

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[10] TROTTER, A., Pugillo di Galle Roccolte dal Dr. A. FORTI in Asia Minor. Marcellia **9**:193–197. 1911.

[11] KIEFFER, VON, und HERBST, P., Ueber Gallen und Gallenthiere aus Chile. Cent. f. Bakt. Paras. u. Infek. **29**:696–704. 1911.

[12] FELT, E. P., Gall midges of *Aster*, *Carya*, *Quercus*, and *Salix*. Jour. Econom. Ent. **3**:347–356. 1911.

[13] PATCH, EDITH M., Gall aphids of the elm. Bull. No. 181, Maine Agric. Experiment Station. 1911.

[14] SMITH, E. F., BROWN, N. A., and TOWNSEND, C. O., Crown gall of plants; its cause and remedy. Bur. Plant Industry, Bulletin 213. 1911.

[15] NORTON, J. B. S., Crown swelling disease of peach. Phytopathology **1**:53, 54. 1911.

unknown causes. The structure of the swelling is characterized by spongy masses of parenchyma filled with starch and interspersed with woody layers.

An interesting myco-cecidia of the orange is described by FLORENCE HEDGES.[16] This cecidia is attributed to *Sphaeropsis tumefaciens*, nov. sp., which is described. The external characters of the gall are given, but the development and histology are omitted.—MEL T. COOK.

Phycomycetes.—PETERSEN gives an abbreviated English translation of his paper on the aquatic Phycomycetes of Denmark, which was originally published in Danish. The paper[17] is divided into three parts, the first dealing with the phylogeny and relationships of the Phycomycetes, the second with their occurrence and distribution, and the third with descriptive taxonomy.

As to their phylogeny, the author adheres to the view that the aquatic Phycomycetes and their near relatives constitute a phylogenetic series. If they were derived from the algae at various levels, they would hardly show the homogeneity which runs through the aquatic forms. As to the direction of their evolution, he holds that the lower Phycomycetes have been derived from the higher forms through reduction of the plant body. This view, which necessitates the assumption that motile zoospores and cilia were acquired by the degenerating forms, meets with difficulty when the non-aquatic Peronosporales are considered. The author regards the Pythiaceae, on account of their probable relationship with *Lagenidium*, as the ancestors of Lagenidiaceae. The Peronosporales, to which the Pythiaceae belong, would therefore form a part of the reduction chain, and it would be necessary to assume that zoospores adapted to aquatic conditions have arisen among the aerial Peronosporaceae from conidia eminently suited for aerial distribution. The alternate hypothesis that the Peronosporaceae are losing their aquatic characters in a dry habitat, instead of acquiring them, seems more reasonable. The chief argument of the author is directed against the view of FISCHER that the Phycomycetes are derived from the Monadineae. Here he rightly points out, among other differences, that the germinating zoospore of the Phycomycetes leaves the spore membrane behind, while in the endophytic Monadineae the zoospore makes its way in its entirety into the host cell. The author rightly regards the Synchytriaceae as a distinct group, which represents a line of development different from the rest of the Chytridiales. The idea is not fully carried out, however, in his synopsis of the families given later.

In the second part of the paper are given many interesting observations on the biology and distribution of the aquatic Phycomycetes in Denmark. The Saprolegniales occur frequently on fish and frog spawn, but they do not

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[16] HEDGES, FLORENCE, *Sphaeropsis tumefaciens*, nov. sp., the cause of the lime and orange knot. Phytopathology **1**:63–65. 1911.

[17] PETERSEN, H. E., An account of Danish freshwater Phycomycetes, with biological and systematical remarks. Ann. Myc. **8**:494–560. *figs.* 27. 1910.

———, Studier over Ferskvands-Phycomyceten. Botanisk Tidsskrift **29**: 345–429. *figs.* 27. 1909 (with English abstract).

produce such epidemics among fish as have been reported in other countries. Dead twigs, which have fallen into the water near the shore, form the most common habitat for these fungi. They sometimes occur on remains of aquatic plants, like *Nuphar* and *Nymphaea*, but herbaceous plants do not generally seem to be a favorable substratum for their growth. Leaves which fall into the water in autumn are not a suitable subtratum. The lower forms frequently infect plankton crustaceans, which have not generally been regarded as hosts for these fungi. The most favorable time for the growth of the aquatic Phycomycetes is in early spring, while the water is still too cold to allow growth of bacteria and infusoria.

The rest of the paper consists of a taxonomic arrangement of the species, with notes as to their habits and occurrence. The brief descriptions which are given for the known species in the former paper are omitted in the translation, diagnoses being given only for the new species. Of these there are twelve. One, *Pythiomorpha gonapodyoides*, represents a new generic type. It is unfortunate that the designation "sp. nov." accompanies the names of these species in the translation. It is needless to point out the confusion that may result from such double publication of new species in editions appearing nearly a year apart.

The paper, which is an excellent achievement in local botany, shows the results which sustained study of a group may be expected to yield in territory of which the flora is presumably fairly well known. It is to be hoped that it may direct the work of botanists of other countries to this fruitful field.

According to a brief article by MAIRE and TISON,[18] sexuality usually attributed to *Urophlyctis* is lacking in that genus. In *Urophlyctis* empty cells are found accompanying the sporocysts, thus making it appear as if conjugation had taken place. These empty cells, however, according to the authors, are nothing more than the older vegetative cells whose contents have passed into the younger cells, which arise as buds from the older ones. The authors conclude that *Urophlyctis* should be classed with the Cladochytriaceae, the three genera, *Urophlyctis*, *Physoderma*, and *Cladochytrium*, forming a well-defined natural group.

LECHMERE[19] has described the abnormalities occurring in a species of *Saprolegnia* which he had under observation in pure cultures for a period of five months. The abnormalities, which frequently occur in laboratory cultures of these plants and some of which have been figured by several investigators, occur mostly in the sporangia, and cause these organs to assume forms and modes of behavior characteristic of other genera of the Saprolegniales. Variations are described simulating the sporangia of *Leptomitus*, *Pythiopsis*, *Achlya*,

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[18] MAIRE, RENÉ, et TISON, ADRIEN, Recherches sur quelques Cladochytriaceae. Compt. Rend. **152**:106, 107. 1911.

[19] LECHMERE, A. F., An investigation of a species of *Saprolegnia*. New Phytologist **9**:305–319. *pls. 1, 2*. 1910.

Dichtyuchus, and *Aplanes* in form, manner of discharge, and germination of spores. A common type of variation is one in which chains of rounded sporangia discharging laterally are formed. It is well to have these variations recorded from observations on a single form in pure cultures.—H. HASSELBRING.

Photosynthesis in water plants.—BLACKMAN and SMITH[20] have published two papers upon "Gaseous exchanges of submerged plants," being nos. 8 and 9 of the excellent series on "Experimental researches on vegetable assimilation and respiration" issued from BLACKMAN's laboratory. The first of the present papers deals with "A new method for estimating the gaseous exchange in submerged plants." Instead of using the oxygen elimination as the basis for study, the CO_2 consumed is determined. Water of known CO_2 content (determined by tritation) is passed over submerged plants of a given illuminated surface, and the CO_2 withdrawn for photosynthesis determined by later titration. Correction is made for CO_2 produced by respiration and for that in the eliminated gas. The method seems to insure reasonable accuracy.

In agreement with other workers, BLACKMAN and SMITH find *Elodea* extremely sensitive to adverse conditions. A few days of storage in tap water in laboratory or greenhouse cuts the assimilation 17 to 30 per cent. The plant also endures great concentration of CO_2. Water saturated from an atmosphere containing 30 per cent CO_2 does not interfere with assimilation; it is not likely that air plants would long endure such concentrations. The points of large significance can be set forth by quotations from the summary of the second paper:

"The aim of this study is to demonstrate the *nature* of the relation between assimilation and the chief environmental factors: (1) CO_2-supply, (2) light-intensity, and (3) temperature. The relation is such that the magnitude of this function in every combination of these factors is determined by one or the other acting as a limiting factor."

"The identification of the particular limiting factor in any definite case is carried out by applying experimentally the following general principle. When the magnitude of a function is limited by one of a set of possible factors, increase of that factor, and of that one alone, will be found to bring about an increase of the magnitude of the function."

"The experiments in this paper deal with such moderate intensities of assimilation as may be fairly well maintained for several successive hours. With more intense assimilation the values soon fall off by the action of internal factors grouped at present as the *time factor*. Experiments in which this additional factor has to be reckoned with will be considered in a later paper."

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[20] BLACKMAN, F. F., and SMITH, A. M., Experimental researches on vegetable assimilation and respiration: VIII. A new method for estimating the gaseous exchanges of submerged plants; IX. On assimilation in submerged water plants and its relation to the concentration of carbon dioxide and other factors. Proc. Roy. Soc. London B **83**:374–412. 1911.

The work from BLACKMAN'S laboratory has done much to substitute a physico-chemical conception for the too general stimulus conception of the German plant physiologists. In this direction these papers again bring forth evidence for the non-existence of true optima, for the great importance of "limiting factors," and for the significance of what BLACKMAN has designated as the "time factor."—WILLIAM CROCKER.

Cytology of the ascus.—The controversy to which the behavior of the ascus nucleus has recently given rise, has led GUILLIERMOND[21] to reinvestigate the subject. Contrary to the results of Miss FRASER[22, 23, 24] and her coworkers, these new observations extend and entirely confirm his previous studies, and convince him that the number of chromosomes remains constant during the three successive mitoses of the ascus nucleus. He discusses the method of formation and the separation of the chromosomes of the first division, and whether there exists a second numerical reduction during the third nuclear division. In all of the species studied (*Humaria rutilans*, *Peziza catinus*, *Pustularia vesiculosa*, *Galactinia succosa*), he finds that the number of chromosomes of the equatorial plate stage and of the anaphases remains the same, and that the distribution of these chromosomes is accomplished in the same way in all of these forms. As in previous studies, GUILLIERMOND[25, 26] believes that the process described by MAIRE[27, 28] that is, a double longitudinal division of the chromosomes during the anaphases, which results in doubling the number of chromosomes found in the equatorial plate stage, rests on incorrect observations. He also believes that MAIRE'S contention that there exists in the ascus of *Galactinia succosa* protochromosomes, which fuse into four definite chromosomes, is untenable. GUILLIERMOND holds that there are eight definite chromosomes and not four, which are formed directly and not from protochromosomes. These eight chromosomes are divided only during the meta-

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[21] GUILLIERMOND, M. A., Aperçu sur l'évolution nucléaire des ascomycètes et nouvelles observations sur les mitoses des asques. Rev. Gén. Botanique **23**:89–120. 1910.

[22] FRASER, H. C. I., Contributions to the cytology of *Humaria rutilans*. Ann. Botany **22**:35–55. 1908.

[23] FRASER, H. C. I., and WELSFORD, E. J., Further contributions to the cytology of the ascomycetes. Ann. Botany **22**:465–477. 1908.

[24] FRASER, H. C. I., and BROOKS, W. E. ST. J., Further studies on the cytology of the ascus. Ann. Botany **23**:538–549. 1909.

[25] GUILLIERMOND, M. A., Recherches sur la karyokinèse des ascomycètes. Rev. Gén. Botanique **16**:1–65. 1904.

[26] ———, Remarques sur la karykinèse des ascomycètes. Ann. Mycol. **3**:344–361. 1905.

[27] MAIRE, R., Recherches cytologiques sur quelques ascomycètes. Ann. Mycol. **3**:123–154. 1905.

[28] ———, Recherches sur la karyokinèse chez les ascomycètes. Rev. Gén. Botanique **16**:130–143. 1904.

phases, and not again during the anaphases. The exact manner of division of the chromosomes seems to agree with that described by Miss FRASER, but on the basis of certain stages, which he thinks were missed by her, he interprets his results in a different way. He describes a synapsis stage, whose loops correspond to the V-shaped chromosomes, which later appear on the spindle in the equatorial plate. Although he does not very strongly insist on this point, he is inclined to think that the scheme of chromosome reduction described by FARMER and MOORE for higher forms of plants and animals obtains in the ascomycetes. In the first part of the paper an interesting discussion of the state of these questions and other problems relating to the ascomycetes will be found.—J. B. OVERTON.

Anaerobic growth.—LEHMAN[29] has studied anaerobic growth in higher plants, trying to determine whether the view of WIELER or that of NABOKICH is correct. WIELER claims that the higher plants will not grow in total absence of oxygen, but that only a very low oxygen pressure is needed for growth. NABOKICH claims that higher plants will grow in absence of oxygen. He maintains, however, that proper nutritive conditions must be supplied, as in fungi. For this purpose a glucose solution is suitable. This solution certainly increases anaerobic growth in the pea seed, sunflower seedling, and other forms. In a later article, not cited by LEHMAN, NABOKICH[30] describes the course of anaerobic growth in higher plants. Soon after placing the organ in the oxygen-free medium, growth ceases (Vacuumstarre). Somewhat later growth begins, and the rate rises until it equals that of aerobic growth. Still later growth ceases and death of the organ ensues. NABOKICH explains the course of anaerobic growth as follows: oxygen acts as a stimulus to growth, and not merely as an energy releaser, hence with its withdrawal growth ceases; intramolecular respiration later produces poisonous by-products, which in low concentrations act as stimuli to growth, but which with further accumulations stop growth and kill the organ. The bad feature of this explanation is the indefiniteness of the term stimulus. NABOKICH finds that resting plant cells or those with low metabolic activity can remain in oxygen-free condition for long periods without injury.

LEHMAN found only very slight if any anaerobic growth in *Vicia Faba*, *Pisum sativum*, *Lupinus albus*, *Brassica Napus*, *Phaseolus multiflorus*, and *Cucurbita*, either in distilled water or glucose solution. In *Zea Mays* and *Glyceria fluitans*, anaerobic growth was marked in glucose solution, but was nil in distilled water. In *Helianthus annuus*, anaerobic growth was slight in distilled water, but considerable in glucose solution. LEHMAN concludes that anaerobic growth in any higher plants is not long-enduring nor considerable

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[29] LEHMAN, ERNST, Zur Kenntnis des anaeroben Wachstums höheren Pflanzen. Jahrb. Wiss. Bot. **49**:61–90. 1911.

[30] NABOKICH, A. J., Ueber die Wachstumsreize. Beih. Bot. Centralbl. **26**:7–149. 1910.

when compared with aerobic growth. He also finds no coincidence between intensity of "intramolecular" respiration and of anaerobic growth. The conclusions of these workers are drawn from too few and these mainly cultivated forms. Study of wild forms of varied habits may show very different results. —WILLIAM CROCKER.

Structure of the spore wall.—A notable addition to our knowledge of the structure and development of the spore wall is contributed by BEER[31] in a study of the young pollen grains of *Ipomea purpurea*. At the conclusion of the reduction division, the tetrads of young pollen grains become surrounded by massive mucilaginous walls, which show the reactions of callose and pectose. Within this mucilaginous wall, and surrounding each young pollen grain, is another mucilaginous wall with the same reactions. This second wall is called the "special wall," a term suggested by STRASBURGER to replace the awkward and misleading term "special mother cell wall." The exine is deposited by the pollen protoplast upon the inner surface of the special wall, and at first is homogenous, but soon becomes differentiated into an outer lamella, with a network of thickening bands on its inner surface, and at the intersection of the bands are the rudiments of the spines. At this stage a clear space is seen between the outer lamella and the thickening bands, and in this space the rodlets characteristic of the mature pollen develop. The spines project into the pollen cavity before they begin to appear externally. The intine develops within the exine as a thin layer, with thicker portions where it protrudes into the exit pores. Chemically, it consists of pectic bodies associated with some cellulose. In older pollen grains the exine consists of a delicate outer lamella perforated with countless pores, so that it really forms a reticulum with open meshes, beneath which are the thickening bands constituting the mesospore, perforated by the narrow exit pores for the pollen tubes. The outer lamella of the exine dips into the exit pores and covers the protrusions of the intine at these spots. Since nearly the entire growth of the rodlets and spines takes place after they have become separated from the protoplast, it is concluded that they are able to develop without any direct contact with the protoplasm.

This short paper presents a thorough study of a single species and suggests a series of investigations, for it may be predicted with the utmost confidence that the account will not hold for angiosperms in general, and the author makes no such claim. After various types of pollen grains have received similar attention, it will be time to generalize.—CHARLES J. CHAMBERLAIN.

Chemotaxy.—SHIBATA[32] gives the first part of a full statement of his extensive work on chemotactic responses of the spermatozoids of pteridophytes. This

[31] BEER, RUDOLF, Studies in spore development. Ann. Botany **25**:199–214. *pl. 13.* 1911.

[32] SHIBATA, K., Untersuchungen über die Chemotaxis der Pteridophyten Spermatozoiden. Jahrb. Wiss. Bot. **49**:1–60. 1911.

part deals with positive reactions, while the second part will deal with the negative. SHIBATA himself has contributed no small part of the knowledge in this field, especially with the forms *Isoetes*, *Salvinia*, and *Equisetum*. The paper is divided into seven sections dealing with the following phases of the subject: (1) introduction and methods, (2) action of organic acids, (3) action of metallic ions, (4) action of H and OH ions, (5) action of alkaloids and other organic bases, (6) application of the Weber-Fechner Law, (7) the classes of chemotactic sensibility and their relation to each other.

The body of facts is so great that no statement of it can be attempted here. Some of the generalizations, however, especially those derived from the seventh section, are of considerable interest. SHIBATA concludes that there exists in the pteridophytes three categories of positive chemotactic sensibility: (1) for the anions of malic acid and of the related dicarboxyl acids, (2) for the OH ion (only in *Isoetes*), (3) for cations of metals and hydrogen and for alkaloids. The three categories are entirely independent, as indicated by the lack of antagonistic action between members of different categories. Within the same category one member dulls the action of any other. In general, the dulling effect is proportional to the attractive value, but this is not always the case. Citrate, which is 1/10 as powerful in attracting *Salvinia* sperms as is maleate, is just as effective in dulling the action of maleate as is maleate itself. SHIBATA believes that in chemo-perception within a given category either the first links or at least early links in the chain of perception are identical. He contrasts this situation with that found by KNIEP in certain bacterial forms, who concluded that each individual substance is separately perceived. He found no dulling action between any two chemotactically active substances.—WILLIAM CROCKER.

Coremia formation by Penicillium.—By methods which at the present stage of plant physiology appear somewhat crude and superficial, WÄCHTER[33] has attempted to find the factors influencing the formation of coremia in a form of *Penicillium*, which he designates by the usual name of *P. glaucum*, but which can be easily identified as *P. expansum* Link. The method of study consisted in growing the fungus on sterilized slices of various fruits and vegetables, and on the expressed juices of these, and also on an inorganic nutrient solution with various concentrations of sugar, this being the only medium approximating anything like known conditions. When the results are sifted, we are left in the same position as before as to the factors which influence the formation of coremia, namely, that when grown on various substrata of unknown composition this form (like other coremia-forming species) sometimes forms coremia and sometimes not, a fact, moreover, clearly formulated by THOM[34] in regard to this and other species of similar habit. The work of

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[33] WÄCHTER, W., Ueber die Koremien von *Penicillium glaucum*. Jahrb. Wiss. Bot. **48**:521–548. 1910.

[34] THOM, CH., Cultural studies of species of *Penicillium*. U.S. Dept. Agr., Bur. Animal Industry, Bull. 118. 1910.

THOM, however, came to the author's hands only in time to be noted in the proof. A closer approximation to definitely known conditions, if not yielding positive results, might at least have resulted in excluding certain groups of factors as having no influence on the formation of coremia.

In the latter part of the paper, the author distinguishes 11 forms of *Penicillium* by their growth characters on the substrata which he used in the first part. The forms are not further characterized nor identified with other descriptions. The author lays stress on cultural characteristics, and the utilization of the coremia-forming habit for separating the species of *Penicillium*. Both have been used by THOM in his partial monograph of the group. —H. HASSELBRING.

Feed containing smut spores.—The feeding of grain products containing large quantities of smut spores to animals has usually been regarded as pernicious, both on account of the widespread belief, supposed to be based on practical experience, that the smut spores are injurious to animals, and on account of the danger that the spores pass uninjured through the animal body and, as asserted by BREFELD, become a source of infection when they are distributed over the fields in manure. These questions have been reinvestigated by HONCAMP and ZIMMERMANN,[35] who as a result of feeding experiments, in which large quantities of smut spores, mostly of *Tilletia caries* with some of *T. laevis*, were fed to different domestic animals for long periods of time, came to the conclusion that in no case could any injury be definitely attributed to the smut spores. The spores which had passed through the bodies of animals, with rare exception, were incapable of germination. Further experiments showed that sound spores mixed with manure or other fertilizers and scattered over the soil rarely cause infection of grain. These experiments indicate that the danger of infection from smut spores scattered over the fields in manure has been largely overestimated. This is true more particularly of the spores that have passed through the animal body. The only source of infection to be regarded of significance in agricultural practice is that from the spores adhering to the seed grain, a fact which may be inferred from the almost total prevention of smut by treatment of the seed grain.—H. HASSELBRING.

Temperate plants in Helgoland.—Since the spring of 1904, KUCKUCK has been experimenting with the introduction into Helgoland of various species of plants of warm temperate climates.[36] Although situated but 30

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[35] HONCAMP, FR., und ZIMMERMANN, H. (unter Mitwirkung von G. SCHNEIDER), Untersuchungen über das Verhalten von Brandsporen im Tierkörper und im Stalldünger. Centralbl. Bakt. II. **28**:590–607. 1910.

[36] KUCKUCK, P., Ueber die Eingewohnung von Pflanzen wärmerer Zonen auf Helgoland. Bot. Zeit. **68**[1]:49–86. *pls. 1–3. figs. 2.* 1910.

km. from the mainland, this island enjoys many of the features of an insular climate. February, the coldest month, has a mean temperature of only 1°.34 C., and the lowest temperatures of the winter seldom exceed −8° C. This is much milder than the climate of the mainland, but less genial than that of the southern coast of England. Notwithstanding the favorable temperatures, many plants are injured by the severe and incessant winter winds, and by the lack of a protective covering of snow. KUCKUCK describes his results in detail, indicating the successful culture in the open of a large number of species, including such plants as *Pittosporum Tobira*, *Camellia japonica*, two species of *Fuchsia*, and various opuntias. Perhaps the most noteworthy of them is the fig, *Ficus carica*, which has been cultivated on the island for thirty years, attains a height of 4.5 meters, and matures fruit regularly. KUCKUCK considers in general that the winds are more hostile to plant life than the frosts, and believes that other species might prove hardy if they could be given soils better suited to their requirements.—H. A. GLEASON.

Twining.—NIENBURG[37] has made a detailed study of the nutation movements of young twining plants in their early stages of circumnutation. He believes that all the circumnutation and twining movements can be explained by the joint action of autonomic nutation and negative geotropism. He also believes that he has entirely disposed of NOLL'S conception of lateral geotropism. A careful analysis of his results, however, shows that lateral geotropism will also explain all movements he describes, with the possible exception of one on the centrifuge. The strongest evidence for NOLL'S conception was gained from the use of the centrifuge, and now with a slight alteration of the position of the plant NIENBURG obtains results on this instrument that seem to disprove NOLL'S conception. NIENBURG'S centrifuge experiments have their main value, however, in showing the need of further centrifuge studies in this field.—WILLIAM CROCKER.

Amphibious polygonums.—A recent paper very plainly shows that extensive experimental cultures will be necessary before the taxonomic and ecological relationships of the various species of *Polygonum* can be settled. NIEUWLAND[38] distinguishes at least three closely related species of this interesting genus which exhibit both an aquatic and a terrestrial form, but adds no experimental data to our present scanty fund. The species described vary so much in response to varying conditions of habitat that it seems possible that all these forms, with intermediate gradations, might be produced from the same stock by careful methods of culture. An interesting historical résumé of the litera-

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[37] NIENBURG, WILHELM, Die Nutationsbewegungen junger Windepflanzen. Flora **102**:117–146. 1911.

[38] NIEUWLAND, J. A., Our amphibious Persicarias. Amer. Midland Naturalist **2**:1–24. 1911.

ture shows that our knowledge of the ecology of these plants has advanced but little beyond the observations recorded by JOHN RAY[39] more than two centuries ago.—GEO. D. FULLER.

Syndiploid nuclei.—Nuclear figures in chloralized root tips, described by NĚMEC, then by STRASBURGER, and then discussed and figured at some length in NĚMEC's recent book on fertilization, have been reinvestigated by STRASBURGER.[40] He used again the root tips of *Pisum sativum*, and made a critical comparison of the nuclear figures in normal and chloralized tips, and compared the peculiar mitoses of syndiploid nuclei with the normal heterotypic mitoses of the same species. He agrees with NĚMEC that the syndiploid nuclei gradually disappear, but denies that any heterotypic mitoses are concerned in the disappearance. NĚMEC's figures, intended to support the theory of a somatic heterotypic mitosis, are discussed and explained as only peculiar vegetative mitoses, with merely superficial resemblances to genuine reduction divisions. —CHARLES J. CHAMBERLAIN.

Structure of protoplasm.—During the last decade cytologists have been so busy with various phases of the chromosome problem that little attention has been given to the structure of protoplasm. A preliminary announcement by LEPESCHKIN[41] is entitled "On the structure of protoplasm," but this paper deals with artificial emulsions rather than with protoplasm itself. The principal conclusion is that streaming protoplasm cannot have the foam structure described by BÜTSCHLI, but rather has the structure of an emulsion. He admits that the peripheral layers of protoplasm in infusoria may have a foam structure.—CHARLES J. CHAMBERLAIN.

Peat bogs in Iowa.—A comparison has been made by PAMMEL[42] between the peat bogs of northern Iowa and those occurring in other parts of the United States. The principal types found in this state are the aspen bog, willow bog, sedge bog, and rush bog, none having a very extensive development. The sphagnum bog is conspicuously absent. A detailed comparison of the bog flora of Iowa, Wisconsin, and Michigan shows that in Iowa many of the typical bog plants of more northern regions are replaced by others of a very different character.—GEO. D. FULLER.

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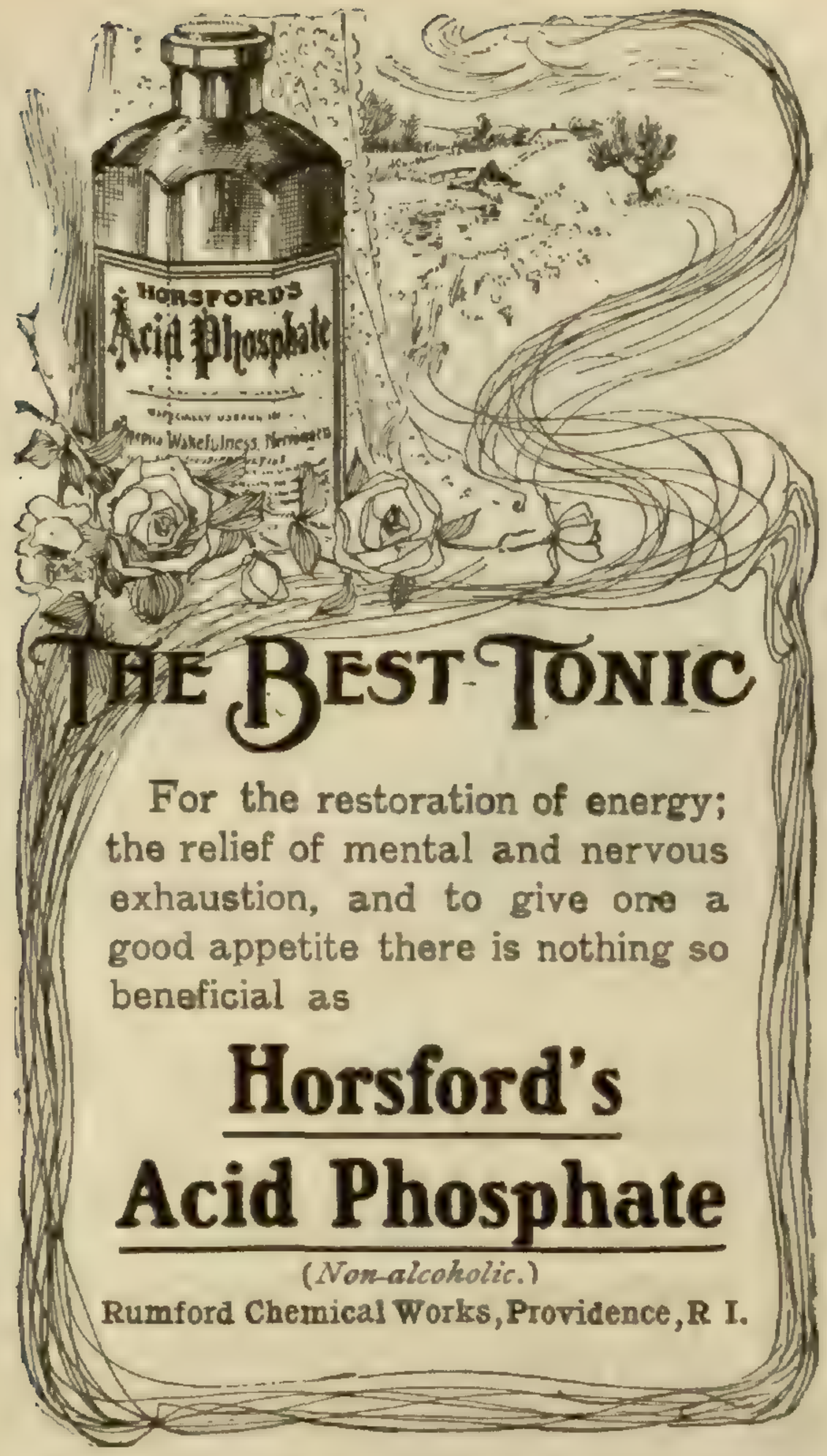
[39] RAY, JOHN, History of plants. Vol. I, p. 185. 1686.

[40] STRASBURGER, EDUARD, Kernteilungsbilder bei der Erbse. Flora **102**:1–23. *pl. 1*. 1911.

[41] LEPESCHKIN, W. W., Ueber die Struktur des Protoplasmas. Ber. Deutsch. Bot. Gesells. **29**:181–190. 1911.

[42] PAMMEL, L. H., Flora of northern Iowa peat bogs. Iowa Geol. Survey **19**: 739–784. 1909.



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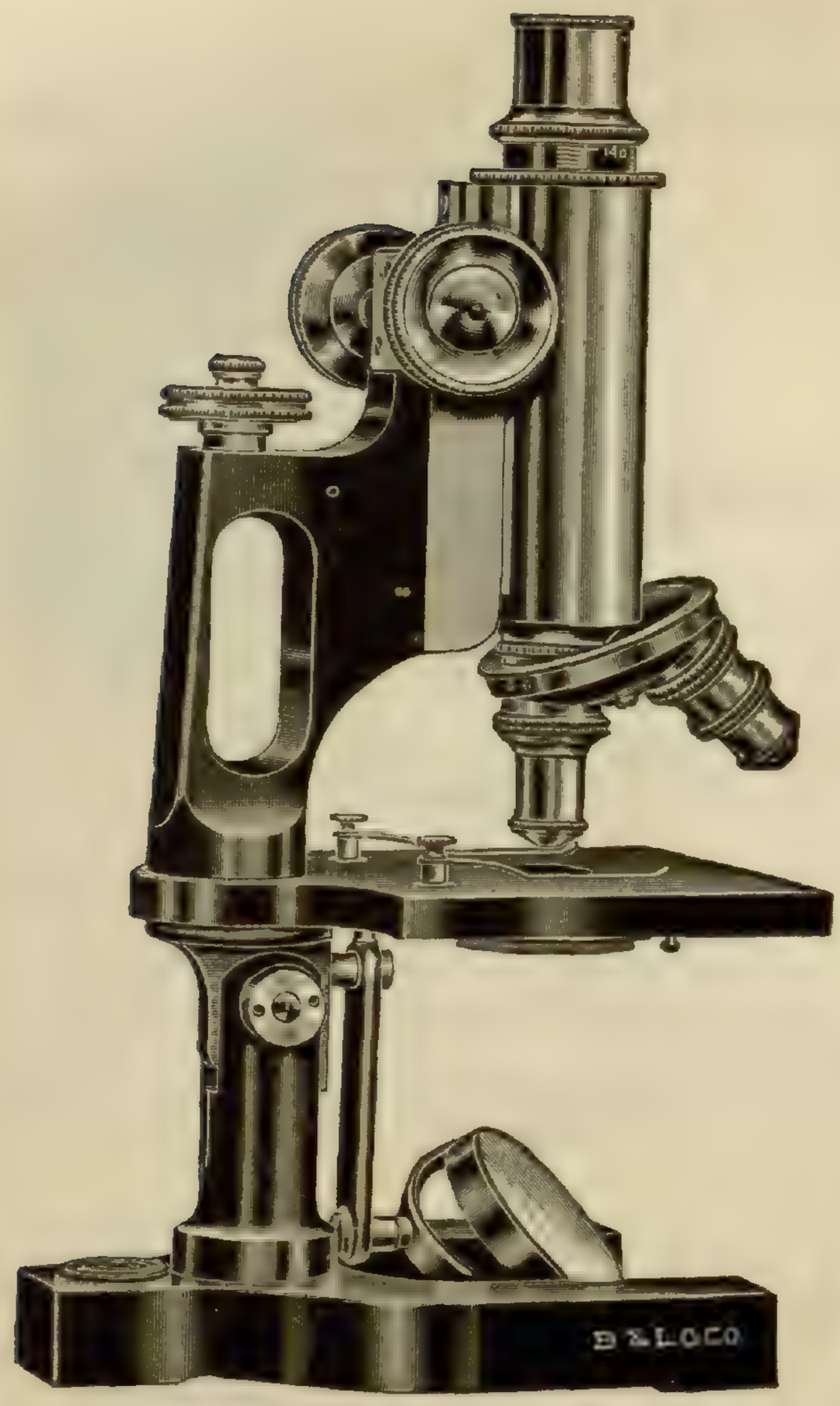

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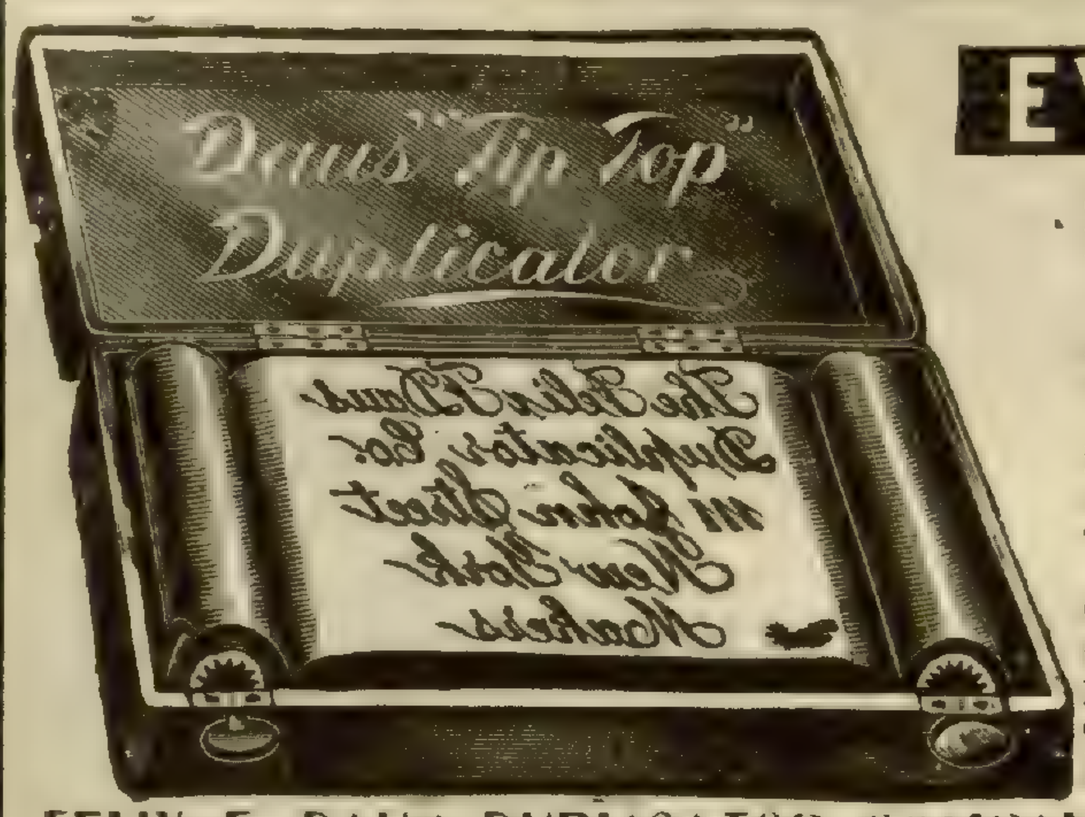

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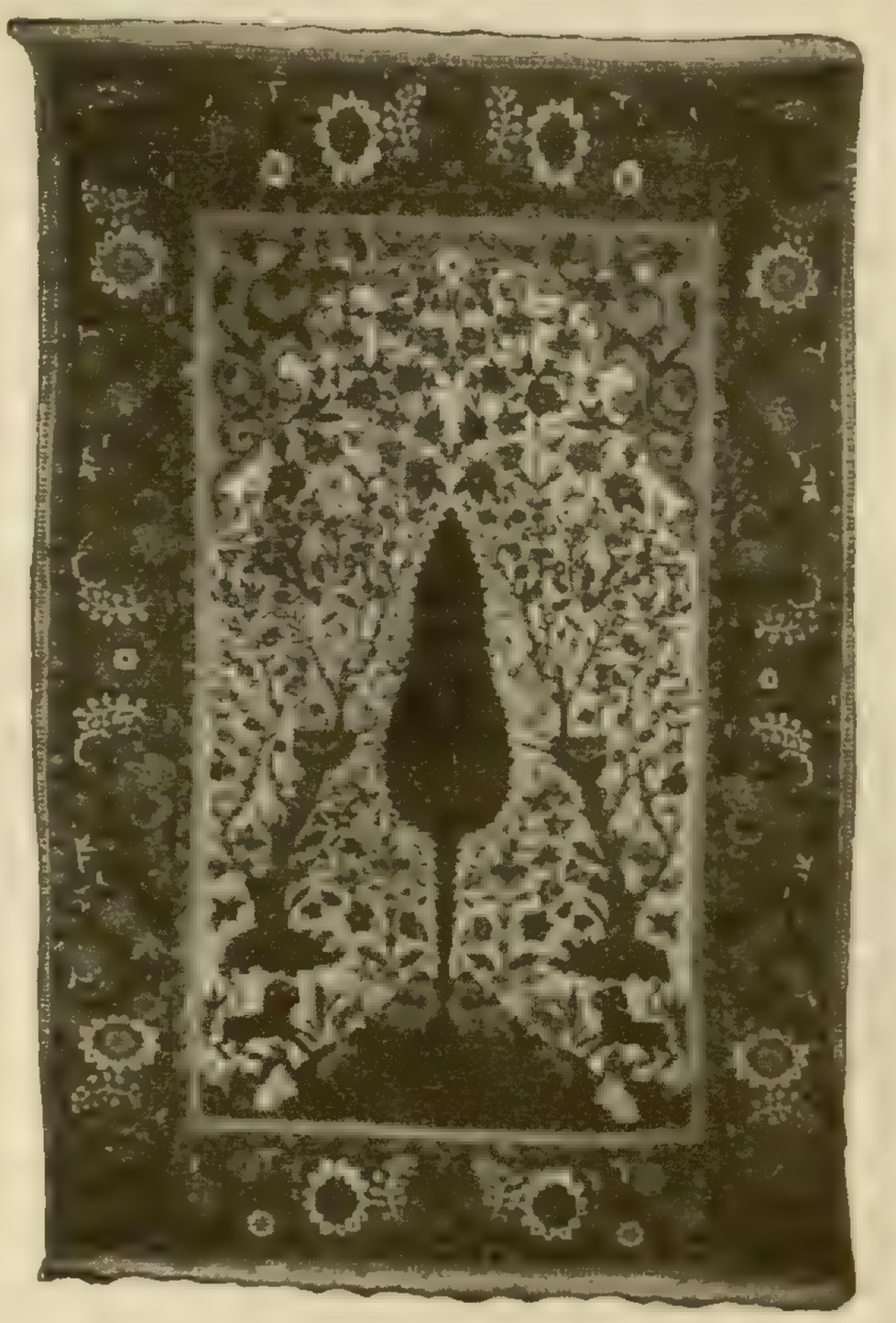

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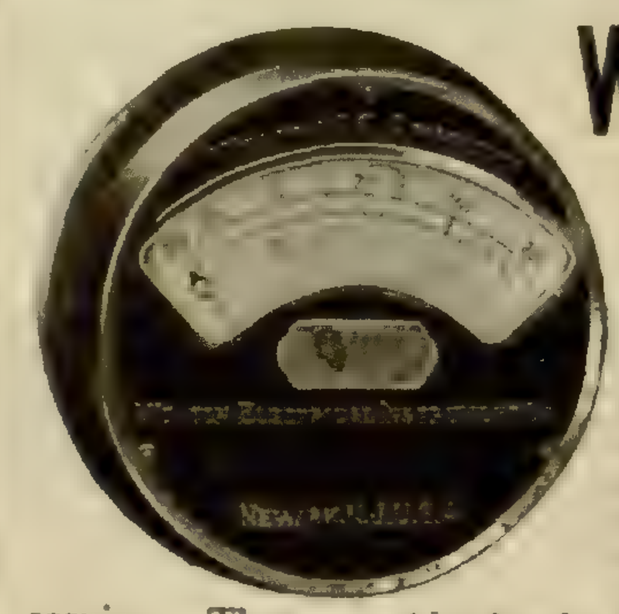

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VOLUME LII NUMBER 4

THE
BOTANICAL GAZETTE
OCTOBER 1911

AN ATTEMPTED ANALYSIS OF PARASITISM

D. T. MACDOUGAL

(WITH SIX FIGURES)

According to a recently published estimate made by the author, about half of the total number of seed plants use complex food material derived from other organisms by mycorhizal or parasitic arrangements. So far as our observations go, dependent species, which are advantaged by contact or association with other species, undergo direct somatic modifications, consisting chiefly of atrophies or reductions of the shoot and root system; and in plants of fixed parasitic habit, these reductions may be such as to include the total disappearance of the roots and to bring the shoot down to simple, unbranched, chlorophylless stems, upon which the leaves are represented by colorless bracts. The fruits and seeds may show various specializations.

During the course of an extensive investigation of the conditions under which two species may enter into the relation of host and parasite, regenerated cuttings of a large number of species were attached to the stems of desert succulents and xerophytes. In some cases the attached plants formed roots; and in others the epidermal cells performed the function of absorption.

The ruling factor was in all cases the osmotic ratio between the sap of the two plants; one plant may not become parasitic upon another except by the aid of a superior osmotic pressure which withdraws solutions from the tissues of the enforced host. Many causes, however, may operate to prevent a potential parasite

from becoming actual, such as the formation of wound-cork, excretions, periodic alterations in turgidity, etc. The physiological alterations consequent upon the arrangement of two plants in a xeno-parasitic relation are of a saltatory or mutative character, yet no evidence is at hand as to the manner in which such alterations become fixed and transmissible. A perfectly graded series of parasites may be selected which exemplify all stages of dependency, atrophies or reductions, and adjustive arrangements; but nothing may be assumed as to the manner in which progress has been made from one stage to another. It seems fair to conclude, however, that the evolutionary movement is generally toward increased dependency of the parasite, accompanied by accentuated and more complete atrophies. The view that such a movement may sometimes ultimately lead to extinction, although by a long and indirect way, seems also justifiable by inference, although such an end must not be assumed for all groups of parasites.

FIG. 1.—*Cissus laciniata* parasitic on *Opuntia Blakeana;* the host has been sectioned to expose the roots of the xeno-parasite.

In the experiments carried on at the Desert Laboratory from 1908 to 1911, the desert grape (*Cissus laciniata*) of Mexico, the expressed juice of which shows a pressure of over 11 atmospheres, was found to maintain itself on the flattened joints of *Opuntia Blakeana* at about 9 atmospheres; not so successfully on *Echinocactus Wislizeni*, the drinkable juice of which has a concentration equivalent to about 6 atmospheres; while it soon perished when attached to stems of the great tree cactus (*Carnegiea gigantea*) at less than 7 atmospheres (fig. 1). The last named plant exudes an acrid fluid from fresh wounds, which are quickly closed by the formation of heavy, corky layers. *Opuntia versicolor*, a species with cylindrical stems showing a pressure of 12 atmospheres, was able to draw supplies for extended periods from *Carnegiea* and the other hosts mentioned. Plantlets of *Agave* were equally efficient, although this xeno-parasite formed such a great number of roots as to destroy the tissues of the host plant. *Cissus* also formed roots which penetrated the host, while the absorptive contact of *Opuntia* (flat-stemmed) was by the epidermal cells of the stems in every case examined.

The briefest inspection of the results of the analysis of plants used in these experiments, shows that the direct proportion of mineral salts in the sap and the acid contents of the sap have no direct bearing on possible parasitism among the higher plants.[1] The relation of seasonal cycles, capacity for development of absorptive elements *de novo*, and an accommodative adjustment of the osmotic pressure of the cell sap are to be mentioned as factors in the making of nutritive couples. The greater number of the parasitic arrangements made are to be included with the root parasites.

A few additional experiments were set up to test certain points after the completion of the manuscript printed in 1910. The results of these and of the continuation of older preparations seem to warrant the presentation of this additional note on the subject.

May 11, 1910.—A number of beans of a mixture of species native to the deserts of southern Arizona were attached to joints

[1] See MACDOUGAL and CANNON, The conditions of parasitism in plants. Publ. No. 129, Carnegie Inst. of Wash. 1910.

of prickly pear, with the radicles thrust into cavities in the soft tissue. The bean was held in place by a setting of plaster of Paris, and a moist strip of cloth was brought from a vessel of water to furnish moisture until the plants should become established in their new relations.

May 13.—A large number of new insertions of the "rusty" bean in joints of *Opuntia* and bodies of *Carnegiea* and *Echinocactus* were made on this day. Some of the original preparations were showing notable growth.

May 14.—Some of the plants first arranged had thrust the tips of the plumules beyond the cotyledons, but had not yet straightened the hypocotyl. One bean with wilted plumule was taken out of the *Opuntia*. The main root had grown but little. A secondary branch from near its base had come out and extended down into the cavity, alongside the main root, showing as great a length.

May 22.—Twelve seedlings on *Opuntia* had survived, of which one had developed the plumule to an extent that the leaves were unfolding from between the cotyledons. Six seedlings on *Echinocactus* had survived, and were showing some slight development. Three seedlings out of 9 insertions on *Carnegiea* had survived and had made a slight development. The cotyledonary curvature was still markedly present.

May 31.—Temperatures of 111° and 112° F. out of doors, and all parasites were flagging, apparently dying. All soon perished.

About a dozen germinated beans of the form known as "small Papago white" were inserted in joint of "Mission Pear" (*Opuntia* sp.), near the laboratory at Carmel, California, on June 23, without any protection except a cloth shade. These, with the exception of two, dried out, although small secondary roots were formed by June 27. All were replaced and a small vial was arranged with a strip of cloth to give shade and moisture. About 8 similar preparations were arranged on *Oenothera biennis* and *O.H.206*. On July 1, only one of this lot had become dry, the fogs of the preceding days having been an obvious advantage.

July 14.—Seven Papago white beans on Mission Pear thriving, of which three had well developed leaves of the first simple pair.

and one showed a second pair. The others still retained the plumule partly between the cotyledons.

August 2.—All beans were dead or nearly so. All of the development in these plants was undoubtedly carried on at the expense of material in the cotyledons; and the roots soon perished after being immersed in the mucilaginous tissues of *Opuntia* or the stems of *Oenothera*. The high humidity of the fogs and low temperatures ranging between 45° and 65° F. also made for the endurance of the seedlings. These tests are chiefly interesting in contrast with the cultures of PEIRCE, in which plants of *Pisum sativum* were grown on stems of *Vicia Faba* to maturity. The advantage of the aeration of the roots in the central cavities of the stems of the host and also of one legume parasitic upon another, doubtless accounts in large measure for the success of these cultures.[2]

The completion of the original manuscript on this subject left several preparations in good condition, which were two years old. Among these were *Opuntia Blakeana*, *O. versicolor*, *O. arbuscula*, and *O. leptocaulis* on *Carnegiea*; *O. leptocaulis* on *O. discate*; also one *Agave americana* on *Carnegiea*. Some of these parasites remained alive throughout a part or all the year, it being noted that those shielded from direct illumination by the body of the host survived longest. March 1911 found arrangements of *Opuntia versicolor*, *O. Blakeana*, and *Agave* on *Carnegiea*.

All these preparations were made with plants as xeno-parasites which were characterized by a water balance of some amount and by an osmotic pressure of the sap of 9–12 atmospheres. Furthermore, the survivors were held in place by a mass of plaster of Paris molded about the bases of the stems which held the roots closely appressed against the corky tissues of the host.

This state of affairs may be seen to furnish a fair approximation of the physical conditions under which an *Opuntia* was found with the roots in a small cavity in the trunk of a *Parkinsonia*, and of the same species in a cavity in the summit of a trunk of *Carnegiea*.[3] A further illustration is offered by a case photographed and reported

[2] PEIRCE, G. J., Artificial parasitism, etc. BOT. GAZ. **38**: 214. 1904.

[3] See Publ. No. 129, Carnegie Inst. of Wash. 1910.

FIG. 2.—*Cissus laciniata* and *Opuntia* growing from sinus in stem of *Yucca*, near Tehaucan, Mex.; an epiphytic bromeliad is attached to one of the terminal joints of the *Opuntia*.

by Dr. W. A. CANNON, in which a flat-jointed *Opuntia* was found established in a cavity in the trunk of an *Acacia Greggii*. One or more species of *Opuntia* native to the Tehuacan region find a foothold in the crevices of tile roofs, and stone and adobe walls, in a very noticeable manner; and it was in this vicinity that one of these plants and a native grape were found rooted in the sinus of a forked tree *Yucca* (fig. 2).

The conditions of such association seem favorable for the slow extraction of solutions from the host plant through non-living tissues without the actual contact of the living cells, an approximation to the initial conditions of parasitism. It is obvious that the crowded root systems of a wide physiological variety of plants in the soil furnish numberless duplications of these conditions, and it seems entirely reasonable to suppose that such contiguity of absorbent and succulent roots may acccount, in part, for the greater number of root parasites.

It is to be noted that among the higher plants the part played by destructive secretions is at a minimum. The activity or absence of such substances in seed parasites has been variously described. In no instance, however, are there such abundant and disintegrating effects as may be seen resulting from bacterial and fungal parasites of plants and animals.

The parasitic arrangements described above, in which the host furnishes lodgment and a slowly yielded supply of solution, are characterized by a slow growth of the parasite, in which the amount of development is limited, the members being reduced. The *Opuntia* parasitic on *Parkinsonia*, which was described in *Publication No. 129*, Carnegie Inst. of Washington, 1910 (see pl. 10), was taken from the host early in 1910 and set in the adobe soil of the terraces in the courtyard of the Desert Laboratory. In the course of the growing season of that year, it made three new joints, each of which was three or four times the bulk of those previously formed, the total growth in the previous 7 or 8 years. Furthermore, in this autophytic growth it developed characters which demonstrated that it properly belonged to *Opuntia Toumeyi* instead of *O. Blakeana*, with which it was first identified, because of its small joints and atrophied spines (fig. 5).

The *Opuntia versicolor* which had been fastened in a cavity in the side of a tall *Carnegiea* early in 1909, lost three of its four short branches and the terminal section of the stem during the dry foresummer of 1910. Activity in the rainy season in the midsummer following resulted, not in the formation of additional sections or members, but in the increase in thickness of the stem

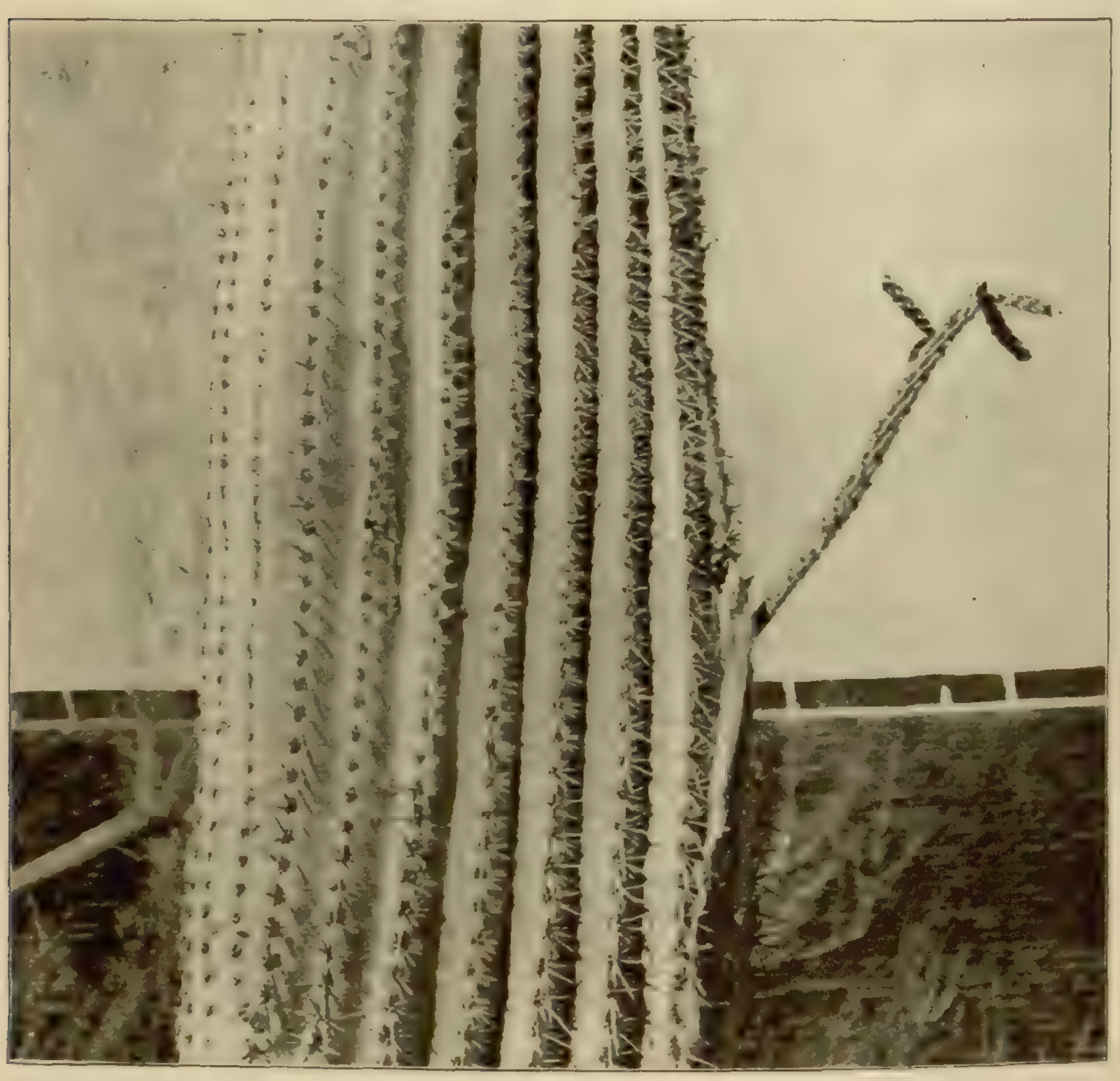

FIG. 3.—*Opuntia versicolor* parasitic on *Carnegiea gigantea*, March 1910

and roots; the latter were thin and fibrous when the preparation was made, January 23, 1909. After two years of parasitic existence, the visible portions of the root system were much enlarged, after a manner sometimes exhibited by autophytic individuals of the same species (figs. 3 and 4).

An *Opuntia Blakeana* set in a cavity of *Carnegiea*, where it was held by plaster, early in 1909, likewise formed no additional

members during the following two years. Some thickening of the cylindrical basal segment, however, was noticeable.

The work described in this and previous papers has been successful in the demonstration of certain physical conditions which make parasitism possible, and has led to the suggestion of physiological activities which limit or facilitate the adhesion of two seed plants in a dependent nutritive combination. Wider observations would doubtless increase the known parasitic combinations, while it may be safely assumed that present conditions are as favorable for their making as at any time in the history of the plant world. New parasites may be expected to be brought to our attention from time to time.

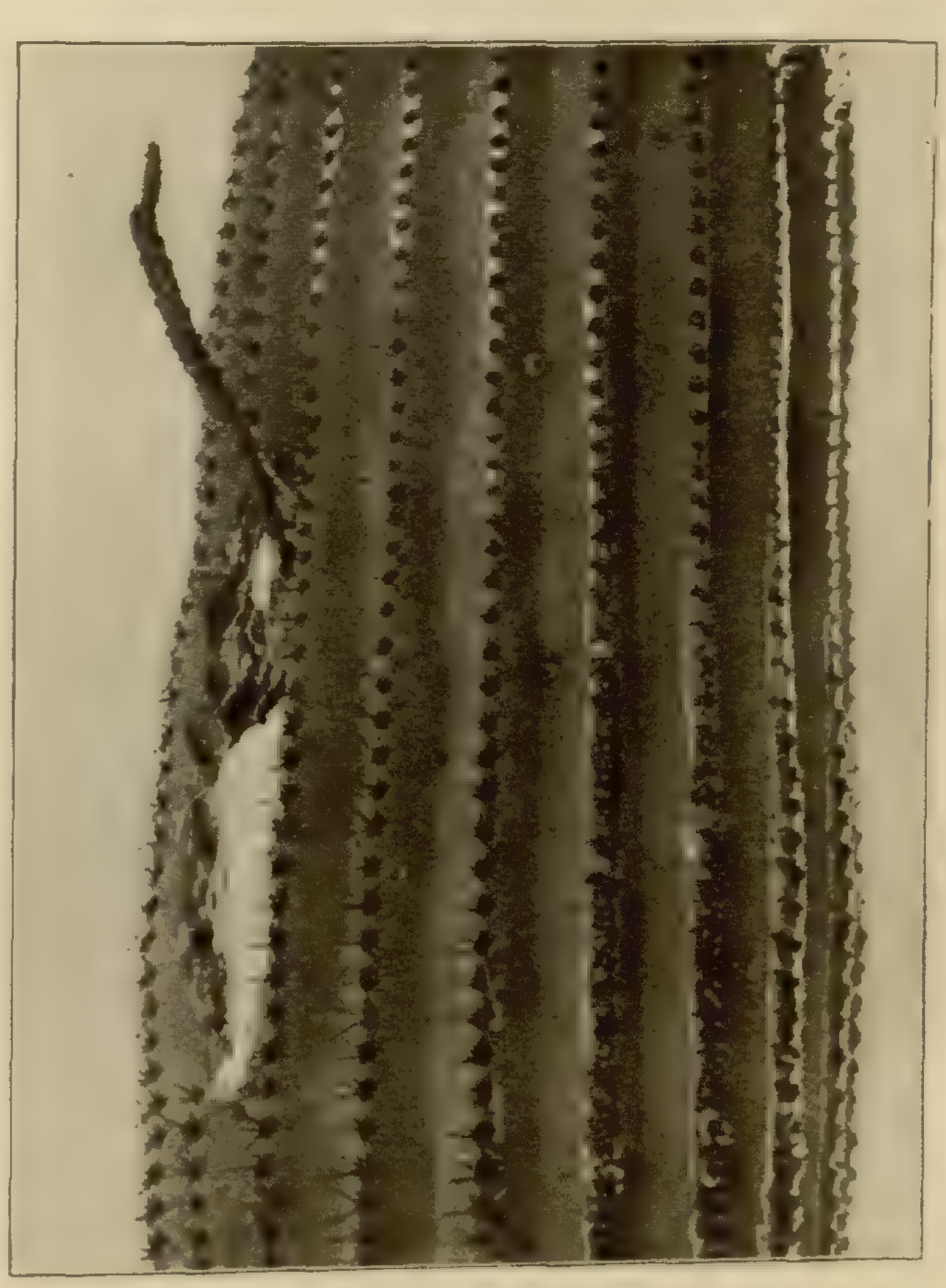

FIG. 4.—Same plant as in fig. 3, March 1911, with enlarged roots and stem, and with but one surviving branch.

The assumption of a mutualistic or dependent rôle, in fact any departure from a purely autophytic condition by a green plant, is inevitably followed by reductions or atrophies. Such combinations are displayed by a number of seed plants, not far short of half the existing species. It is of interest to note that the parasitical consequences have not yet been seen in green plants furnished with food material including organic compounds. The total reaction is complex, and the exciting causes are probably not simple. Whatever they may be, they are furnished only by the living or decaying bodies of other organisms. The part played by the pathological effects and physiologic reactions of parasites in

the evolutionary development of plants has never been adequately portrayed, even in a speculative manner.

The vigor of growth, widely varied capacity for reproduction. range of endurance to unfavorable conditions, and accommodational adjustment displayed by parasitic fungi and bacteria in general seem to place the greater majority of these forms in a

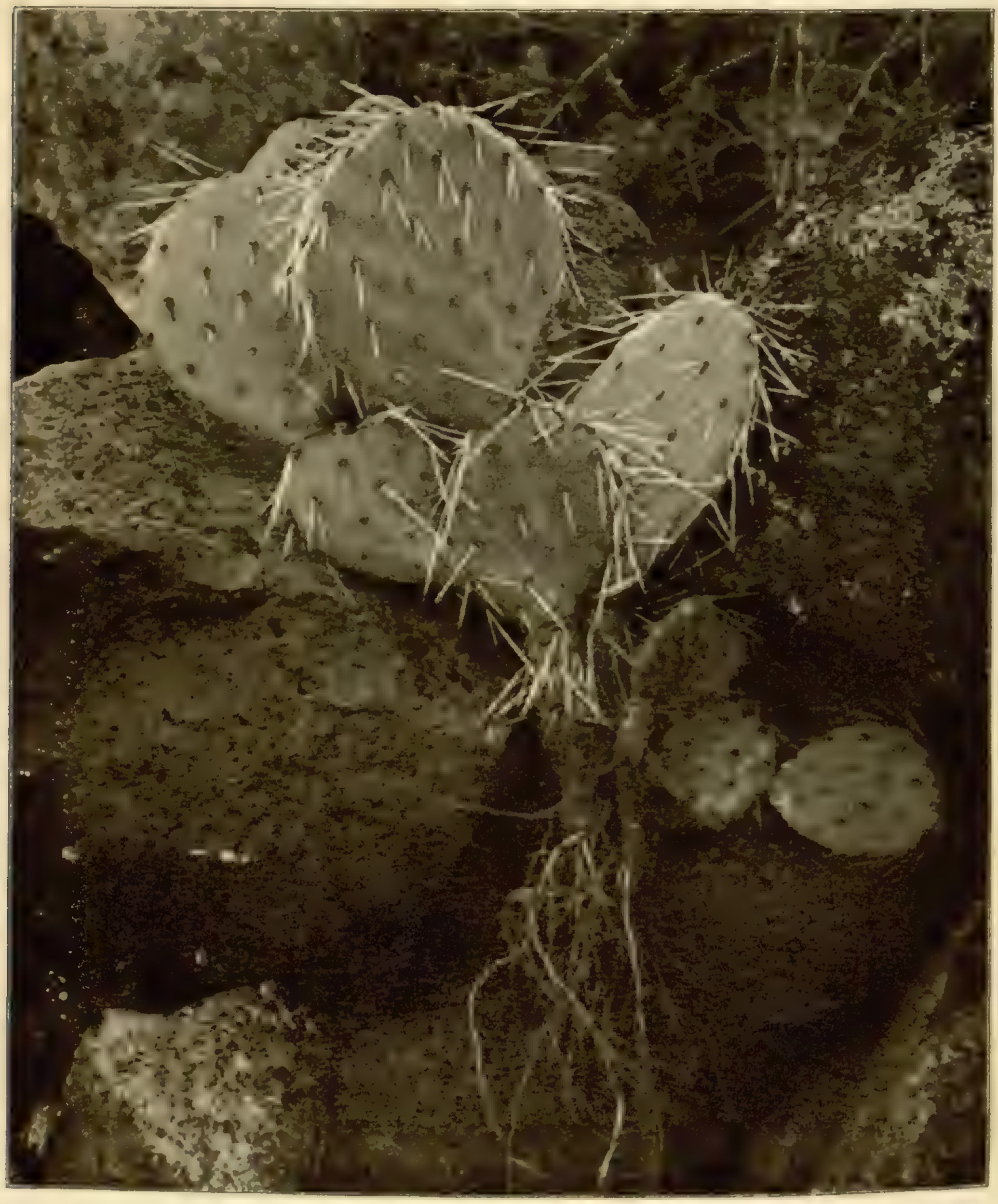

FIG. 5.—*Opuntia Toumeyi;* this plant was found growing in a cavity of the trunk of a small tree of *Parkinsonia microphylla* in 1906, and the small joints formed during its parasitism are to be seen near the base and to the right; the larger joints were developed after the plant began an autophytic existence rooted in the soil; photographed February 1911.

position where the only obvious way to extinction would be by the destruction of their hosts, resulting from their own effectiveness. Nothing known of the life history of any of these forms suggests a possible abandonment of the parasitic habit and of an advancing morphological development. So far as the higher plants are concerned, the only consideration hitherto given to parasitic forms has been to view them as passing down an inclined plane of atrophies, which would ultimately lead to their extinction, without reference to the abundance of development of the host forms. No hint has yet been obtained as to the possibility of a retracement, by which a dependent might once more regain its standing as an autophyte.

FIG. 6.—*Cissus laciniata* parasitic on *Opuntia Blakeana* (see fig. 2).

Regressive action of this character would naturally be discernible only in a series of material extending over long periods of time, such as that obtained by the paleontologist. It is interesting to note that this subject is one to which some serious attention has been given, and Dr. J. M. CLARKE[4] has recently summarized the information with regard to the case of the limpet and the

[4] The significance of certain early parasitic conditions. Science **33**: 291. 1911.

crinoid of earlier times and the gastropods and sea urchins of the present. It is made clear by CLARKE that the limpets of the early Silurian were largely parasitic on the crinoids, a habit that persisted for millions of years, until the closing stages of the Paleozoic, when evidences of it were lost, and no traces of parasitism of snails on the few crinoids of the present are known. Other gastropods of the limpet structure are now parasitic on the starfish and sea urchins, close relatives of the crinoids. The earlier limpets were not carried beyond the stage of possible regression in their parasitism, but the modern parasitic gastropods are "often so modified by their degeneracy that their nature is hardly recognizable, and this parasitism is fixed and beyond repair." Two separate cases of adaptational adjustments seem involved, and the parasitism of the modern gastropods is taken to be wholly independent of the earlier assumption and abandonment of the habit. The suggestion lies near, however, that a family which has thus furnished two separate series of parasites is one which by morphological characters or physiological tendencies is liable to assume dependent relations with other organisms as hosts. Parasitism among the higher plants of the present time is confined to ten families, one of which has been added recently to the list by the work of Dr. W. A. CANNON. It may be safely assumed that in some of these, the Orobanchaceae, for example, the habit is far beyond retraction.

DESERT LABORATORY
TUCSON, ARIZONA

CONTRIBUTION FROM THE ROCKY MOUNTAIN HERBARIUM. IX

NEW PLANTS FROM IDAHO

AVEN NELSON

Most of the plants considered in this paper were collected in Idaho. Since they were secured during a single season by an amateur, a word concerning the collector and the field investigated will not seem out of place. Early in 1910 specimens were received from J. FRANCIS MACBRIDE for determination. In the correspondence that developed it was soon apparent that he was a close observer and deeply interested in the flora of his neighborhood and state. A proposition from him to collect for the Rocky Mountain Herbarium led to the discovery that he was a boy just out of the Boise High School. An agreement was soon reached whereby he was to undertake field work in some part of Idaho.

To determine the least worked and therefore the most inviting field, appeal was made to the two men who probably know the flora of the state better than any others, namely the former professor of botany at the University of Idaho, L. F. HENDERSON, and Professor ELIAS NELSON of the Experiment Station. These were agreed that southwestern Idaho was practically unexplored, particularly the whole Owyhee region including the mountains of that name. Their judgment has been confirmed by the work thus far carried out, and further collections in this very interesting field will be made in 1911.

ERIOGONUM OVALIFOLIUM Nutt.—As the collections of this so-called "aggregate" species multiply, the probability increases that the seemingly quite distinct forms of it represent but one very variable species. The type of the species was the comparatively small yellow-flowered form. Then NUTTALL gave us *E. purpureum*, differing in no respect except in color. It has since been shown that between the two the specimens show all shades of yellow to white, and white to purple. At most then, NUTTALL'S second species

ought not to be recognized as more than a variety, and as a recognizable though not necessarily permanent variation.

What is true of *E. purpureum* Nutt. is equally true of three of SMALL'S segregates. They are based on no permanent characters, since in this genus color and size have been shown to vary with every change in the ecological factors. Two of these species, *E. ochroleucum* and *E. orthocaulon*, occur in the semi-arid portion of the Snake River basin and its tributaries. They may grow intermingled in the same district, as was the case in the superb specimens mentioned below. I therefore propose one varietal name to represent the two as follows.

ERIOGONUM OVALIFOLIUM **celsum.**—*E. ochroleucum* Small, Mem. N.Y. Bot. Gard. **1**:123. 1900; *E. orthocaulon* Small, Bull. Torr. Club **33**:53. 1906.

MACBRIDE'S specimens, soon to be distributed under this varietal name, represent well the two colors, the oval to oblong leaves, and the tall scapes. New Plymouth, Idaho, May 21, 1910, nos. 85 and 86.

ERIOGONUM OVALIFOLIUM **vineum.**—*E. vineum* Small, Bull. Torr. Club **25**:45. 1898.

Besides the wine-colored flowers, this is more noticeably tomentose, hence may be kept distinct from the preceding variety, though like that it merely represents the species in its maximum development.

Stanleya rara, n. sp.—Inflorescence inordinately crowded, becoming 4 or more dm. long, the rachis only moderately stout: pedicels about 10 mm. long, in fruit 15–20 mm.: sepals yellow, linear, about 10 mm. long and 1 mm. or more wide: petals yellow, linear, narrower than the sepals and about three times as long; the claw longer than the sepals and but little narrower than the blade: anthers 3–4 mm. long, at length well exserted and more or less curved or coiled: ovary at full anthesis about 4 mm. long, somewhat shorter than its stipe: pods at maturity filiform, 4–6 cm. long or possibly more, irregularly curved and spreading, on stipes nearly half as long and somewhat longer than the pedicels.

This is a tentative description of a seemingly excellent species, and is described from only a fragment of the plant. This had been gathered for a bouquet by Mrs. CROUTHERS, on a dry hillside, near Big Willow post-office, in Canyon Co., Idaho, about May 25, 1910, where it undoubtedly is indigenous.

This fragment is no. 217 in MACBRIDE'S series. He will try to secure the plant in quantity in 1911.

Thelypodium milleflorum, n. sp.—Tall, branching, wholly glabrous, biennial, 1–2 m. high, the stout main axis and the much slenderer ascending branches a deep purple below, becoming paler upward: leaves coarsely and irregularly dentate to entire, passing from oblong below to linear above; the lower petioles 6–15 cm. long, usually shorter than the blades, becoming shorter upward: inflorescence greatly crowded, at length very long (that of the main axis often 4–6 dm.) but even in fruit quite dense: flowers, pedicels, and even the rachis very pale or milky white: sepals narrowly oblong-linear, slightly cucullate and greenish at the tip, about 5 mm. long: petals very narrow, twice as long as the sepals; the spreading blade nearly linear: the clawlike portion filiform but distinctly expanding again near the base: filaments at length well exserted, and the purple, linear, scarcely sagittate anthers coiled: pods a pure green, in good contrast with the pale pedicels and rachis, almost filiform, 6–10 cm. long, normally strongly ascending or suberect, but often irregularly spreading as if from their weight: stipe 2–3 mm. long; the style about the same length: the ascending pedicels a little longer than the stipes.

This is *T. laciniatum* Endl. in part, some specimens being found in herbaria under that name. That species differs from this in many ways, but noticeably its habitat (on rocks), its smaller size, its laciniate leaves, its shorter, thicker, spreading pods, and opener inflorescence with green pedicels and rachis.

The best specimens are MACBRIDE 234, New Plymouth, Idaho; abundant in rich soils on open slopes; in May, and by June in full fruit. It is also represented by CUSICK 1955, from dry bottom lands, Malheur Co., Oregon; BAKER 1020, Eagle Valley, Ormsby Co., Nevada; COTTON 391, Yakima region, Washington.

RORIPA PALUSTRIS (L.) Bess.—In studying MACBRIDE'S collections, I found a variation of this widely dispersed species that is quite noteworthy. This led to an examination of all the available specimens at hand, as well as of those representing what we have been calling *R. hispida* (Desv.) Brit. In this study it became evident that MACBRIDE'S specimens have the size, habit, and general aspect, and the perfect glabrateness of *R. palustris*, but

the globose or subglobose pods of *R. hispida*. One is therefore driven to the conclusion that these are but variations of one species.

In the present disturbed condition of nomenclature, one scarcely knows what generic designation to employ. However, if one ignores names prior to 1753, the order of the three names commonly employed seems to be *Roripa* Scop., Fl. Carn. 520. 1760; *Radicula* Dell. ex Moench, Meth. 262. 1794; *Nasturtium* R. Br. Ait., Hort. Kew. Ed. 2. **4**:109. 1812.

Following the same plan on the specific name it seems to result as follows:

Roripa terrestris (R. Br.), n. comb.—*Nasturtium terrestre* R. Br., *l.c.*; *N. palustre* DC., Syst. **2**:191. 1821; *Roripa palustris* (L.) Bess., Enum. 27. 1821.

RORIPA TERRESTRIS **hispida,** n. comb.—*Brachylobus hispidus* Desv., Journ. Bot. **3**:183. 1814; *Nasturtium hispidum* DC., *l.c.*; *Roripa palustris hispida* Rybd., Contrib. U.S. Nat. Herb. **3**:149. 1895.

RORIPA TERRISTRIS **globosa,** n. var.—Tall and often declined, 4–10 dm. high, perfectly glabrous; pods globose or subglobose, with a short necklike constriction between pod and receptacle.

MACBRIDE 275 is typical; swampy land, Falk's Store, Canyon Co., Idaho, June 22, 1910; also by AVEN NELSON, Head of Wood's Creek, Albany Co., Wyoming, August 1910.

Spiraea idahoensis, n. sp.—A shrub, wholly glabrous throughout, 10–18 dm. high, branched below; the current year's branches erect, 3–5 dm. long and very leafy: bark of young branches very pale reddish brown: leaves large, ovate to elliptic or often oval, usually rounded-obtuse at both ends but sometimes subacute at apex, nearly regularly serrate often almost to the base, 5–9 cm. long: panicle large, more or less compound, cylindrical or pyramidal, the lower branches of the panicle axillary to the uppermost somewhat reduced leaves: calyx lobes reflexed, triangular-ovate, mostly acute, about as long as the disk: petals rose color, about 2 mm. long, twice as long as the calyx lobes, ovate, subacute or obtuse: filaments slender, more than twice as long as the petals: carpels ovate-oblong, smooth and polished, about 0.5 m. long.

It is singular that this Idaho shrub should so long have passed for *S. Menziesii* Hook. That species finds its typical development along streams and

in cold bogs of the Northwest. It is always more or less pubescent, and its leaves are typically narrower and smaller. Its Idaho counterpart is a shrub of the mountains or foothills, in moist soil but not in marshy or wet places. *S. idahoensis* is reported plentiful throughout southern Idaho.

The type is MACBRIDE 630, collected at Trinity, Elmore Co., August 23, 1910.

Potentilla trina, n. sp.—Perennial from a rough shreddy but slender vertical caudex, 4–8 cm. long, green and glabrate or even quite glabrous: stems less than 1 dm. high, slender but erect, few-leaved and few-flowered: leaves trifoliate: basal leaves on slender petioles 5–8 cm. long; leaflets short-petioled or subsessile, 1–3 cm. long, broadly obovate-cuneate, deeply and incisely toothed, the teeth more or less incised; stem leaves sessile, narrowly cuneate, incisely toothed at apex: cymes very few-flowered: calyx tube sparsely and minutely hirsute; sepals triangular-lanceolate, about 5 mm. long, acute, obscurely ciliolate; bractlets oblong, mostly obtuse, shorter than the sepals: petals obovate, emarginate, 6–8 mm. long: stamens about 20: carpels 20–25.

This is a very near relative of *P. emarginata* Pursh, and may be only a geographical variety of that arctic species. If it stands as a species, it must do so on the strength of its almost glabrate condition, larger and longer rootstocks, larger leaflets, and erect habit.

Collected by MACBRIDE in the Trinity Mountains, on the grassy banks of Star Lake, one of the Trinity Lakes, August 30, 1910, no. 680. Only a few plants were found.

Prunus padifolia, n. comb.—*Cerasus padifolia* Greene, Proc. Biol. Soc. Wash. **18**:59. 1905.

MACBRIDE secured some excellent red cherry specimens on his collecting trip in Idaho in 1910. These led to an examination of GREENE's interesting paper on "Some West American red cherries." A checking up of the specimens in the Rocky Mountain Herbarium in the light of this paper revealed some sheets referable to the above name, including MACBRIDE 443 and 479 from Silver City and Twilight Gulch. He secured two sets of specimens, one typically red-fruited, the other with fruit a clear lemon yellow. Otherwise no differences in the two collections could be seen. A character not mentioned by GREENE is the glandular denticulation of the leaf margin.

Thermopsis xylorhiza, n. sp.—Stems clustered, erect, rather slender, from a branched woody caudex surmounting a stout woody root, 4–7 dm. high, simple and (at maturity) leafless below, sparingly branched above, glabrate and somewhat striate: green,

glabrous above, very sparsely pubescent beneath; the stipules ovate or obovate, obtuse or acutish, 2–4 cm. long, either longer or shorter than the petiole; leaflets oval to narrowly elliptic, obtuse or acutish at apex, mostly somewhat cuneate at base, 4–8 cm. long: raceme of 10–20 rather crowded flowers; calyx finely pubescent; the campanulate tube 6–7 mm. long, the triangular acute teeth half as long; the deep-yellow corolla more than twice as long as the calyx: the young pods erect, straight, white with fine silky pubescence, at maturity greenish and sparingly pubescent, moderately or only slightly arcuate, spreading, 4–8 cm. long and 5–7 mm. broad; the pedicels 5 mm. or less.

So far as known to the writer, the other western species all have a semi-fleshy running rootstock, but aside from the woody character of the caudex and roots this species has other good characters to distinguish it.

Secured by MACBRIDE at Falk's Store, Canyon Co., Idaho, May 24, 1910, no. 99.

Hypericum tapetoides, n. sp.—Depressed perennial, spreading by the slender rhizome-like stems which root at the nodes, very leafy: leaves glabrous, oval or obovate, tapering to the half-clasping base, 5 mm. or less long, longer than the internodes: flowers rarely solitary terminal, usually in cymes of 3–several: sepals 5, similar, narrowly elliptic-oblong, abruptly acute, about 3 mm. long: petals 5, orange yellow, elliptic, very delicate, 5–7-nerved, as long as or longer than the sepals, marcescent: stamens 12–20, distinct, nearly as long as the petals: styles 2–4, equaling the stamens, slightly dilated upward to the truncate or subcapitate summit: capsule ovoid, acute, as long as the sepals: seeds numerous, oblong, minutely longitudinally roughened striate.

Very distinct from *H. bryophytum* Elmer, BOT. GAZ. **36**:60. 1903, and from *H. anagalloides nevadense* Greene, Fl. Fran. 113, apparently the only species to which it makes a close approach. It was found growing in dense mats on sunny mossy, boggy stream and lake banks, usually intermingled with mosses and with these forming thick soppy-wet carpets of green. MACBRIDE 453, Silver City, Owyhee Mountains, in bloom, July 22; no. 570, Trinity, Elmore Co., in fruit, August 1910.

SPHAERALCEA RIVULARIS **diversa,** n. var.—Differing from the species in the green and almost glabrous leaves which are shallowly only 3–5-lobed; the lobes mostly obtuse, often broadly rounded,

never sharply serrate on the margin but varying from entire to merely undulate crenate: flowers not crowded-terminal as in the species, but axillary-pediceled in the upper leaves and in a short nearly naked terminal raceme of 3 or 4 flowers: carpels hirsute-hispid on upper part of the back only.

MACBRIDE 582, moist hillsides, Manyon Creek, Elmore Co., August 11, 1910.

Phaeostoma rhomboidea, n. comb.—*Clarkia rhomboidea* Dougl., Hook. Fl. Bor. Am. **1**:214. 1833; *Opsianthes gaurioides* Lilja, Linnaea **15**:261. 1840.

The genus *Phaeostoma* was established by SPACH (Hist. Veg. Phan. **4**:392. 1835), one species being referred to it, namely *P. Douglasii*, which was the earlier *Clarkia elegans* Dougl. I am not so much surprised that this excellent genus was later suppressed (during the Benthamian era) as I am that it has not been since restored. There are only a very few species referable to it, but these are so aberrant in the genus *Clarkia* that one trying to find them by means of keys now available meets with a number of contradictory and misleading statements. *Clarkia rhomboidea* runs just as readily to *Godetia* as to *Clarkia*, for it requires a decided mental bias to recognize the narrowed base of its petals as a claw.

Removing the species with entire petals from *Clarkia*, it becomes homogeneous in that all the species have clawed, 3-lobed petals, only 4 real stamens, and a stigma evidently lobed. *Phaeostoma*, on the other hand, has entire petals with or without claw, eight perfect subequal stamens, and a stigma with lobes so short that the stigma looks capitate or disciform. It is to be noted too that in *Phaeostoma* some of the leaves are opposite. The other species referable to this genus are as follows:

Phaeostoma elegans, n. comb.—*Clarkia elegans* Dougl., Lindl. Bot. Reg. *t. 1575*.

Phaeostoma xanthiana, n. comb.—*Clarkia xanthiana* Gray, Proc. Bost. Soc. Nat. Hist. **7**:145. 1861.

Phaeostoma parviflora, n. comb.—*Clarkia parviflora* Eastwood, Bull. Torr. Club **30**:492. 1903.

Sphaerostigma implexa, n. sp.—Annual, more or less branched from the base and upward, 1–2 dm. high; the stems and branches puberulent and purplish tinged, the bark not exfoliating; the branches ascending, almost as long as the main axis: leaves glabrate or puberulent, oblanceolate to oblong-lanceolate, tapering to a short petiole; the lower 5–7 cm. long, upward passing into the

narrow bracts which are gradually reduced; raceme crowded, becoming narrow and more or less secund, puberulent: calyx lobes lanceolate, 5–6 mm. long, and about twice as long as the tube: petals greenish- or yellowish-white, suborbicular, abruptly acutish, or with a tooth on the subtruncate apex, as long as the calyx lobes: capsule narrowly linear, subcylindrical and only slightly enlarged downward, at maturity 20–25 mm. long and greatly contorted or implexed.

The habit and general appearance of this suggests *S. decorticans* (H. & A.) Small, from which it is far removed geographically and otherwise.

Type, MACBRIDE 27, from Falk's Store, Canyon Co., Idaho, dry stony hillsides, May 17, 1910.

Onagra (OENOTHERA) **ornata,** n. sp.—Stout biennial, widely spreading from the summit of a rather large woody root; the several stems assurgent and simple, 5 dm. or more high, very leafy, densely and finely pubescent, with some scattering ciliate hairs: leaves narrowly oblong-lanceolate to linear-lanceloate, the largest 10–14 cm. long, reduced toward the base and into the bracts (first year leaves not seen), with short dense subcinerous pubescence: inflorescence crowded: calyx densely white hirsute-pubescent, at anthesis its tube less than 4 cm. long, about twice as long as the ovary, its lobes as long as or longer than the tube: corolla a deep golden yellow, unchanged in drying or shading to orange; the petals broadly triangular-obovate or obcordate, as long as the calyx lobes: anthers yellow, 12–15 mm. long; the filaments much shorter than the petals: style not protruding from the bud but elongating and surpassing the stamens as the buds open: capsule pubescent, 2–3 cm. long, somewhat thickened on the angles and only slightly tapering: seeds angled.

This highly beautiful evening primrose, coming as it does from a state supposedly fairly well worked, is a distinct surprise. Doubtless, however, it is an indigenous plant. The excellent key prepared by Dr. R. R. GATES (Mo. Bot. Gar. Rept. **20**:126. 1909) now makes it possible at least to place species of this genus in fairly well-marked groups. This proposed species will be somewhat aberrant in the *O. grandiflora* group. That the present species has nothing in common with the *O. biennis* group is evident not only from GATES'S key, but is attested by the well-known fact that in that group the petals of all the recognized western species (*O. strigosa*, *O. Hookeri*, etc.) become

paler, pinkish or even white, on drying. GREENE is the only writer who has mentioned a western form (California) in which the petals remain yellow, or turn a deeper yellow, but he referred this to the misunderstood *Oenothera grandiflora* Ait., which Miss VAIL (Torreya **5**:9. 1905) has since definitely located for us. It seems strange, however, that neither HOWELL nor PIPER make any mention in their floras of the large-flowered species represented by this and the next.

MACBRIDE reports this species as scattering in the foothills but more abundant upon the adjacent mountain slopes, near Boise, Idaho; no. 262, June 18, 1910.

Onagra (OENOTHERA) **Macbrideae,** n. sp.—Annual, from a rather slender, vertical taproot: stem simple below or sometimes with one or two smaller accessory erect stems from the crown, usually sparingly branched above, 4–8 dm. high, glabrate in appearance but with a sparse crisped pubescence and a few longer ciliations: leaves glabrate or more evidently pubescent, especially on the midrib or veins which are often substrigose; the radical leaves narrowly oblanceolate, tapering above to the acute apex; cauline leaves similar but smaller and passing into the sessile bracts: inflorescence open from the first: calyx lobes nearly glabrous, about 3 cm. long, shorter than the glabrous slender tube, the linear tips short: petals yellow, thin, fading to a deeper yellow or orange red, obovate-obcordate, about 4 cm. long, twice as long as the filaments: anthers more than 1 cm. long: pistil not protruding from the bud, about equaling the petals: capsule moderately fusiform, nearly straight, and 8-costate, 2–3 cm. long: seeds apparently wing-angled.

Two such splendid plants as these by one collector, seem quite an achievement for one season. In so limited a genus, since both are from the same state, one might suspect that they should be united, but that is impossible, for one is a coarse, pubescent, spreading biennial with woody stems and crowded inflorescence: the other a glabrate, erect, herbaceous annual with few and much larger flowers.

That this species is indigenous can scarcely be doubted. It was secured more than 50 miles from a railroad in a practically uninhabited desert area in the Owyhee Mountains, Idaho. It affords me much pleasure to dedicate it to Mrs. C. M. MACBRIDE, who so industriously and discriminatingly assisted her son in the field work during most of the season of 1910. Type no. 473, Twilight Gulch, July 27, 1910.

Dodecatheon dispar, n. sp.—Glabrous throughout, obscurely, if at all, granular-glandular in the inflorescence: rootstock short, thick,

ascending or erect, producing an abundance of fleshy roots: leaves numerous, oblanceolate, tapering gradually into the long, margined base, tapering lanceolately toward the subacute apex also, 2–3 dm. long: scapes 4–6 dm. high, few-flowered (1–6), the pedicels very unequal: calyx tube obconical, about 5 mm. long; calyx lobes linear-lanceolate, longer than the tube: the sinuses broadly rounded: corolla lobes lance-linear, one-half longer than the sepals, the tube very short: stamens distinct and sessile, stout subulate, as long as the sepals: capsule circumscissile near the apex, then splitting at the summit only into 5 valves, each of which opens for a shorter distance in the dorsal suture, ovoid to oblong, equaling the calyx lobes.

Among the operculate species, having distinct anthers, I can find none with which to compare this large glabrous form.

MACBRIDE 672, moist flats near the Trinity Lakes, Elmore Co., Idaho, August 29, 1910.

COLLOMIA GRANDIFLORA **axillaris,** n. var.—Stems slender, cinerous-puberulent, 3–5 dm. high: leaves puberulent: the capitate flower clusters small and few-flowered, on very short foliar-bracted branchlets axillary in most or even all of the leaves, the terminal cluster often not much larger than the others: calyx very glandular.

Collomia grandiflora is thus seen to be exceedingly variable. Any one comparing this variety with material typical of the species would have no hesitation in declaring them remarkably distinct. But with *C. grandiflora diffusa* Mulford before you, and a goodly number of intermediates between the species and the varieties, one hesitates to name it at all. So striking a variation, however, ought to be designated in some way.

MACBRIDE 580 is the type; Trinity, Elmore Co., August 8, 1910, open hillsides. Less well represented by his no. 376, Silver City, July 14, 1910, steep hillsides.

Phlox aculeata, n. sp.—Depressed-caespitose on the intricately slender-branched caudex: stems slender, sparsely crisped, viscid-pubescent, especially above, the internodes short or nearly wanting: leaves densely crowded, filiform, straight or curved, rather rigid and aculeate, the midrib and margins slightly thickened, obscurely puberulent and the uppermost also minutely glandular; usually only 10–12 mm. long but often a few of them are a half longer: flowers solitary or more often 3–5 at the ends of the branchlets, on pedicels 3–7 mm. long: calyx densely glandular-pubescent,

apparently cleft nearly to the base: its lobes nearly linear, scarious on the slightly broadened base, acuminate and aculeate above, 7–8 mm. long: corolla usually a deep pink, shading to lighter or even white; its tube a half longer than the calyx; its lobes narrowly ovate, rounded and obscurely denticulate at summit, about 8 mm. long: style and the longer stamens as long as the corolla tube: capsule large, spreading the calyx lobes apart, 4–5 mm. long: seeds oblong-ovate, rugulose and minutely puncticulate.

It might be referred to the *P. caespitosa* group but for the usually 3–5-flowered cymes which relate it to the *Kelseyi* group (5 species), and of these it is most nearly related to *P. pinifolia* Brand., which is erect and with calyx and pedicels pilose and not glandular.

MACBRIDE tells me this is common on the dry bench lands in the vicinity of New Plymouth, in the Payette Valley. His collection, no. 73, New Plymouth, May 20, 1910, supplies the type.

Phacelia luteopurpurea, n. sp.—Slender annual, sparingly branched from the base and upward, hispidly short-hirsute, 1–2 dm. high: leaves 2–5 cm. long, somewhat irregularly bipinnate, the oblong-linear lobes rarely few-toothed: inflorescence rather densely and conspicuously dark glandular-pubescent: sepals linear, spatulate, as long as the corolla tube and exceeding the mature capsule, hispid as well as glandular: corolla narrowly campanulate; the tube yellow or yellowish, only 3–4 mm. long, more than twice as long as the broadly rounded spreading purple lobes: stamens nearly as long as the corolla tube, inserted in the margin of pocket-like depressions near the base but without any vertical folds: style 2-cleft at apex only: capsule ellipsoidal, 2 mm. or more long; the ovules about 16; the seeds often fewer, irregularly oblong, with fine transverse acute rugulae.

Most nearly related to *P. bicolor* Torr., but at once distinguished by its glandular pubescence and short corolla. These two, with *P. glandulifera* Piper, *P. Ivesiana* Torr., and *P. Fremontii,* are the members of the section EUGLYPTA Wats. (MICROGENETES A. DC.).

The type is MACBRIDE 84, New Plymouth, Idaho, May 21, 1910; sandy soil.

Madronella purpurea (Howell), n. comb.—*Monardella purpurea* Howell, Fl. N.W. Am. 550.—Low, scarcely more than 2 dm. high, the shrubby base freely branched: twigs of the season very numer-

ous, slender, simple, puberulent, 10–18 cm. high, very leafy: leaves entire, oblong or ovate-lanceolate, subacute, rather thick. obscurely puberulent or nearly glabrous, 12–25 mm. long, usually much exceeding the internodes, tapering into a short petiole: head of flowers close, 15–20 mm. high and about as broad; involucral bracts in two rows, the outer only slightly shorter, all obovate: calyx tube about 10 mm. long, minutely hirsute; the small triangular teeth softly hirsute: corolla tube minutely pubescent, distinctly exceeding the calyx, its linear purple lobes about half as long as the tube.

GREENE'S argument (Leaflets 1:168) for discarding the name *Monardella* seems convincing; therefore, I transfer two most excellent species. The above is re-characterized in the light of MACBRIDE'S perfect specimens from Silver City, in the Owyhee Mountains, no. 434, growing in granite soils.

Madronella parvifolia (Greene), n. comb.—*Monardella parvifolia* Greene, Pl. Baker. 3:22. 1901; appearing in COULTER and NELSON'S *Manual* as *Monardella parviflora*, a slip in copying.

LITHOSPERUM RUDERALE **lanceolatum,** n. comb.—*L. lanceolatum* Rydb., Mem. N.Y. Bot. Gard. 1:233. 1900.

There can be little doubt that PIPER is right (Contrib. U.S. Nat. Herb. 11:486. 1906) in replacing *L. pilosum* Nutt. by *L. ruderale* Dougl.; but not in reducing *L. lanceolatum* to complete synonomy. RYDBERG'S name probably should be retained as representing a recognizable variety. The characters on which he relied to separate it specifically from its nearest ally, *L. pilosum*, are characters of degree, mainly size. This character may so readily be accounted for by environment that one is not justified in giving more than varietal significance to it. In the light of most remarkable specimens of this variety secured by MACBRIDE at Big Willow, Canyon Co., no. 110, the salient characters may be restated as follows:

Stems very numerous, stout 4–6 dm. high: the inflorescence paniculately branched, sepals elongating and surpassing the very large nutlets, which are distinctly keeled and provided with a conspicuous flaring white polished collar bordering the broad concave basal scar.

Pentstemon Macbridei, n. sp.—Caudex woody, subterranean: stems several to many from each of the few crowns of the caudex, puberulent, slender, simple, erect, closely and equably leafy, 1–3 dm. long exclusive of the ample inflorescence: leaves puberu-

lent, narrowly linear, tapering to both ends, 3–6 cm. long, all sessile except the lowest which are somewhat reduced in size and short-petioled, the upper passing into the bracts which are gradually reduced upward: the cymose panicle ample, 1–2 dm. long, or often longer, the open, lower branchlets more or less elongated and bearing simple or compound cymes, puberulent as are also the pedicels which are often much longer than the calyx and with a small pair of bractlets: sepals broadly ovate-lanceolate, acute, green and glabrate with subscarious margin, 5–6 mm. long: corolla showy, bluish-purple, gradually dilated, moderately bilabiate, glabrous within and without, its tube 14–16 mm. long, its oval-oblong lobes spreading, about 5 mm. long: anthers saccate, opening only above the middle, glabrous even on the line of dehiscence, sterile filament flattened at apex, wholly glabrous.

This beautiful *Pentstemon* seems not to be closely related to any described species except *P. gracilenta* Gray, from which it is readily distinguished. That has glabrous herbage and is glandular pubescent in the inflorescence. Its leaves are broader and largely basal, upwardly becoming distant and reduced; the relatively smaller and narrower inflorescence is naked-peduncu-late; and the corolla is smaller and the sterile filament more or less bearded.

I take pleasure in naming this for my young friend J. FRANCIS MACBRIDE, who collected so industriously during the summer of 1910. The type is no 105, secured on loamy slopes, near Big Willow, Canyon Co., Idaho, May 27.

Pentstemon perpulcher, n. sp.—Stems few–several from a short thick woody caudex, 4–8 dm. high including the inflorescence, erect or ascending, puberulent below, becoming glabrous above: basal leaves narrowly oblanceolate, 3–10 cm. long. including the tapering base and petiole; cauline linear-lanceolate, with sessile clasping base, reduced upward and passing into the linear bracts: thyrsus crowded or more open, rather narrow and secund, 1–3 dm. long: sepals glabrous, ovate, acute with subscarious and minutely erose margins: corolla blue, mostly less than 20 mm. long, with moderately dilated glabrous throat and oval lobes: anthers dehiscent, glabrous; sterile filament stiffly bearded at the tip, not at all dilated.

I hesitate to designate another species in the *P. glaber* group. Several segregates have already been published by various authors, none of which, however, seems to have anything to do with the specimens in hand. The

characters relied upon to separate the new species are (*a*) the erect slender stems with the narrow leaves and secund thyrse, giving the plant the aspect of *P. unilateralis* Rydb.; (*b*) the pronounced puberulence of the plant below the inflorescence; (*c*) the short corolla, a third shorter than any of the other species of the *P. glaber* group; (*d*) the glabrous anthers; (*e*) the habitat, the plant seemingly much at home on dry banks of the sage brush deserts of western Idaho. All of these characters are directly opposed to the accepted ones of typical *P. glaber* Pursh.

MACBRIDE 80, New Plymouth, Canyon Co., Idaho, May 21, 1910, is the type.

Pentstemon Woodsii, n. sp.—Moderately short pubescent throughout, and more or less glandular upward: stems wholly herbaceous, from the branches of a short woody subterranean caudex, erect, leafy, terminating in a small cyme of three or five flowers: leaves not at all coriaceous, oblong to oblong-lanceolate, acute, ascending, dentate or denticulate except the lower which are smaller than the others and entire, the larger 3 dm. or more in length and much longer than the internodes: sepals narrowly lanceolate, about 10 mm. long: corolla purplish blue, gradually dilated upward, about 3 cm. long, its oval-oblong lobes less than 5 cm. long, finely woolly in the throat on the lower lip: anthers dehiscent through the junction of the two cells but not explanate, finely matted-woolly; sterile filament not dilated at apex, the very tip bearing a few long woolly hairs: style slender, scarcely exserted but surpassing the included stamens.

I would refer the present specimens to *P. montanus* Greene (of which I have seen no authentic specimens) were it not that GREENE says of that "leaves cinerously puberulent, corolla pink-purple, and sterile filament naked." He would hardly have failed to mention the decidedly glandular pubescence of the inflorescence and the thin, not at all leathery, leaves. In TWEEDY'S specimens, cited as the type, it is mentioned that the corollas blacken in drying, which is not the case at all in *P. Woodsii.*

The fine specimens taken as the type were received from Mr. C. N. WOODS, Supervisor of the Sawtooth Forest Reserve, no. 265, for whom it is a pleasure to name the species.

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THE DEVELOPMENT OF THE ASCOCARP OF LACHNEA SCUTELLATA[1]

WILLIAM H. BROWN

(WITH PLATE IX AND FIFTY-ONE FIGURES)

The material upon which the present study is based was collected at Cold Spring Harbor, Long Island, where the ascocarps of *Lachnea* were found in large numbers upon decaying wood in damp places. The ascocarps appear to be frequently produced in crops, as a considerable number of about the same age are often found on a single log. If all of these are removed while still young, a second crop will usually appear in a few days. If now the young ascocarps are removed as they appear, successive crops may continue to be produced for some time. By this means a large number of young stages can be quite easily obtained.

For microscopical study, sections were cut 3–5 μ thick and stained with Flemming's triple or Haidenhain's iron-alum hematoxylin. The latter gave the best results.

Lachnea scutellata has a disk-shaped ascocarp, 2 mm.–1 cm. in diameter, the upper surface of which is covered by the hymenium, which is colored red. The margin and lower surface of the disk are brown and thickly beset with long brown setae. The setae are long, septate hyphae, the outer walls of which are greatly thickened. A cross-section of an ascocarp (plate fig. 1) shows that the inside is composed of densely interlacing hyphae, while the margin and lower surface are covered by a parenchymatous cortical layer consisting of large, thick-walled hyphae which run nearly parallel to each other and perpendicular to the outer surface of the ascocarp. WORONIN (**38**) described the ascocarp of *Lachnea scutellata* as originating in the production of an archicarp, which soon became surrounded by vegetative hyphae that obscured its further development.

[1] Contribution from the Botanical Laboratory of the Johns Hopkins University, No. —.

In the youngest specimens obtained, the archicarp consisted of a row of 7–9 cells, which had just become surrounded by vegetative hyphae. The ascogonium is the penultimate cell of the archicarp, which when mature consists of about 9 cells (plate fig. 3). The ascogonium and all of the vegetative cells are multinucleate. In the youngest specimens the ascogonium was about one-third to one-fourth its size at maturity. There was observed neither at this time nor later any sign of an antheridium, and since in the young specimens the ascocarp consisted of only a few hyphae, it should have been plainly visible even if degenerated. It seems probable, therefore, that no antheridium is present.

Before the ascogonium reaches its mature size, the walls of the vegetative hyphae on the outside of the young ascocarp become thickened, and these hyphae form the outer covering of the ascocarp (plate fig. 2). This covering undergoes no further growth, but remains at the base of the mature ascocarp and forms the first part of the cortex. The hyphae around the ascogonium remain active and give rise, over the ascogonium, to small hyphae which grow out to form paraphyses (plate fig. 3). The same hyphae which give rise to the hyphae producing the paraphyses give off branches, around the region of the paraphyses, some of which grow up and add to the cortex, while others grow out and form setae. As the cells of the setae and cortex reach their mature size, they become greatly vacuolated and the outer walls increase greatly in thickness. When the setae are first formed, they are bent down toward the center of the top of the young ascocarp, and thus form a covering over the developing hymenium (plate fig. 4). When a part of the cortex is once formed, the development of that part ceases, and further additions are made only in the region between the paraphyses and the cortex. The hyphae here remain active and give rise on one side to paraphyses and on the other to setae and more of the cortex of the ascocarp. As this continues, the older setae are carried outward, and finally come to be on the lower surface of the ascocarp. The setae which are formed first are not as long as those which are formed later, so that the setae around the margin of the disk are longer than those on the under surface. As the hymenium increases in diameter, by the production of more

paraphyses and the pushing in of the ascogenous hyphae, which by this time have grown out from the ascogonium, it becomes too large to be covered by the setae and is thus exposed. When this has occurred, the ascocarp has attained its mature form (plate fig. 1). The relation of the various parts of the ascocarp is shown diagrammatically in fig. 1. In this diagram are shown both the ascogonium and asci, whereas the ascogonium always disappears before the formation of asci.

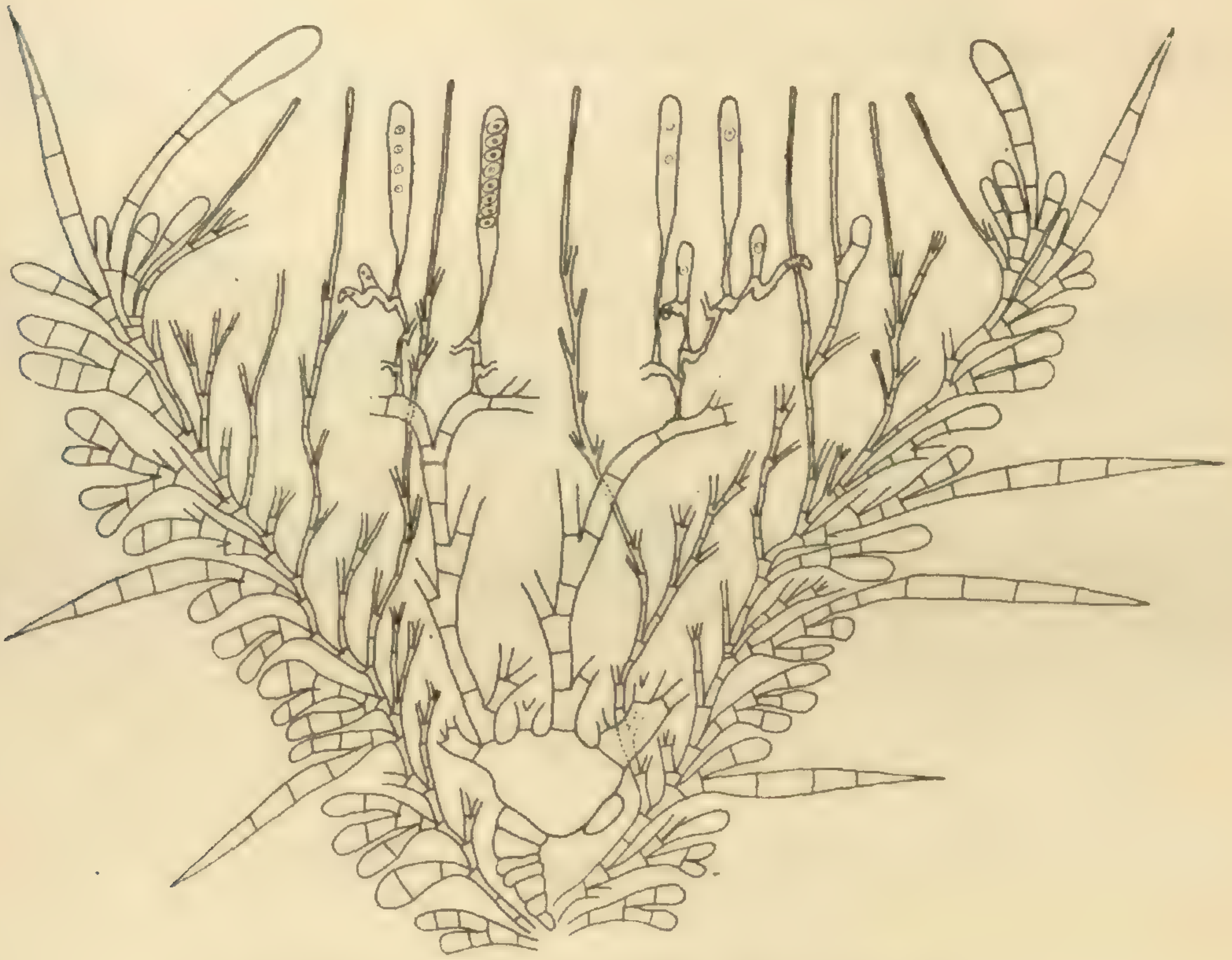
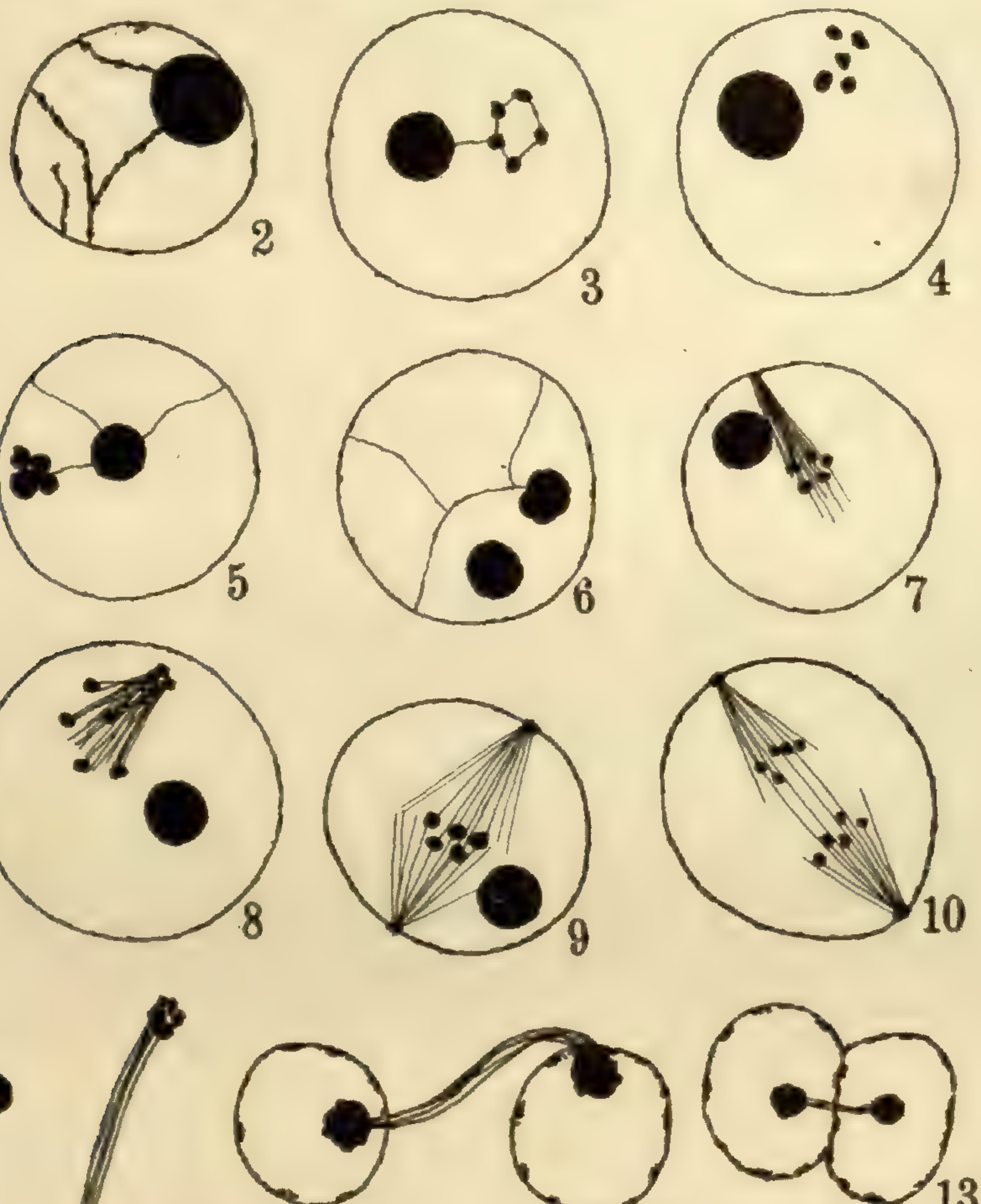


FIG. 1.—Diagrammatic cross-section of ascocarp

The vegetative nuclei usually contain a nucleolus and a small amount of scattered chromatin, but sometimes the chromatin is collected into a rounded mass resembling a nucleolus. In dividing the vegetative nuclei show five chromosomes. The nuclei of *Lachnea* contain comparatively little stainable material, as will be seen from the figures. This scarcity of stainable material makes the figures appear diagrammatic. Such is not the case, however, as all figures were drawn with a camera lucida, and in those illustrating nuclear details, all of the stainable material in the nuclei is

figured. In most cases the cytoplasm is omitted, as this resembles that usually found in Ascomycetes.

The nuclei in the ascogonium resemble the vegetative nuclei



FIGS. 2–13.—Fig. 2, nucleus of ascogonium in resting stage; fig. 3, formation of chromosomes in nucleus of ascogonium; figs. 4–6, arrangement of chromosomes when first found in nucleus of ascogonium; fig. 7, formation of spindle in nucleus of ascogonium; fig. 8, division of centrosome in nucleus of ascogonium; the centrosomes are on the nuclear wall, but owing to their position appear to be inside the nucleus; fig. 9, metaphase in nucleus of ascogonium; fig. 10, anaphase in nucleus of ascogonium; fig. 11, telophase in nucleus of ascogonium; fig. 12, reorganization of nuclei in ascogonium; fig. 13, reorganization of nuclei, in contact, in ascogonium; all ×11,200.

except that they are somewhat larger. The chromatin is usually scattered throughout the nucleus, but sometimes it is arranged in a definite spireme (fig. 2). This condition probably indicates the approach of division. It has not been possible to determine defi-

nitely whether or not the spireme is continuous. Often several loops are tangled together, so that it is impossible to follow individual parts. Still more frequently parts of the spireme run along the nuclear membrane for considerable distances, so that even if it were continuous it could be followed only with considerable difficulty. At other times there appear to be definite breaks. This appearance may be due to a failure of the spireme to take the stain or to poor fixation, but there is nothing to indicate that such is the case. The spireme, soon after its formation, appears to contract and divide to form five chromosomes (figs. 3, 4). The chromosomes may be rather widely separated (fig. 4), but frequently they are collected together into a compact group resembling a second nucleolus (figs. 5, 6). The group can be distinguished, however, from a nucleolus by its irregular outlines. This grouping of the chromosomes is not confined to the ascogonium, but can be seen throughout the ascogenous hyphae and in the prophases of the second and third divisions of the ascus. It is probably also the explanation of the grouping of the chromatin seen in the vegetative nuclei.

While the chromosomes are being formed, linin fibers make their appearance in the nucleus. At the same time a centrosome appears on the nuclear membrane. This was not visible during the resting condition and appears to arise *de novo*. The centrosome is not a point, but rather a flattened area, apparently composed of many granules. When the centrosome was first observed, it was already connected with the chromosomes by the linin fibers in the nuclear cavity (fig. 7). Soon after this the centrosome (fig. 8) divides, and the daughter centrosomes move apart and come to be situated at the opposite poles of the complete spindle (fig. 9). The centrosomes in fig. 8 are against the nuclear membrane, but owing to their position appear in the figure to be within the nucleus. The five chromosomes then divide and five daughter chromosomes proceed to each of the opposite poles (fig. 10). The nuclear membrane now breaks down, and the two groups of chromosomes and the nucleolus, which soon disappears, are left free in the cytoplasm (fig. 11). The two groups of chromosomes are usually separated far enough so that when they reorganize the daughter nuclei are separated by an appreciable distance (fig. 12). Frequently, how-

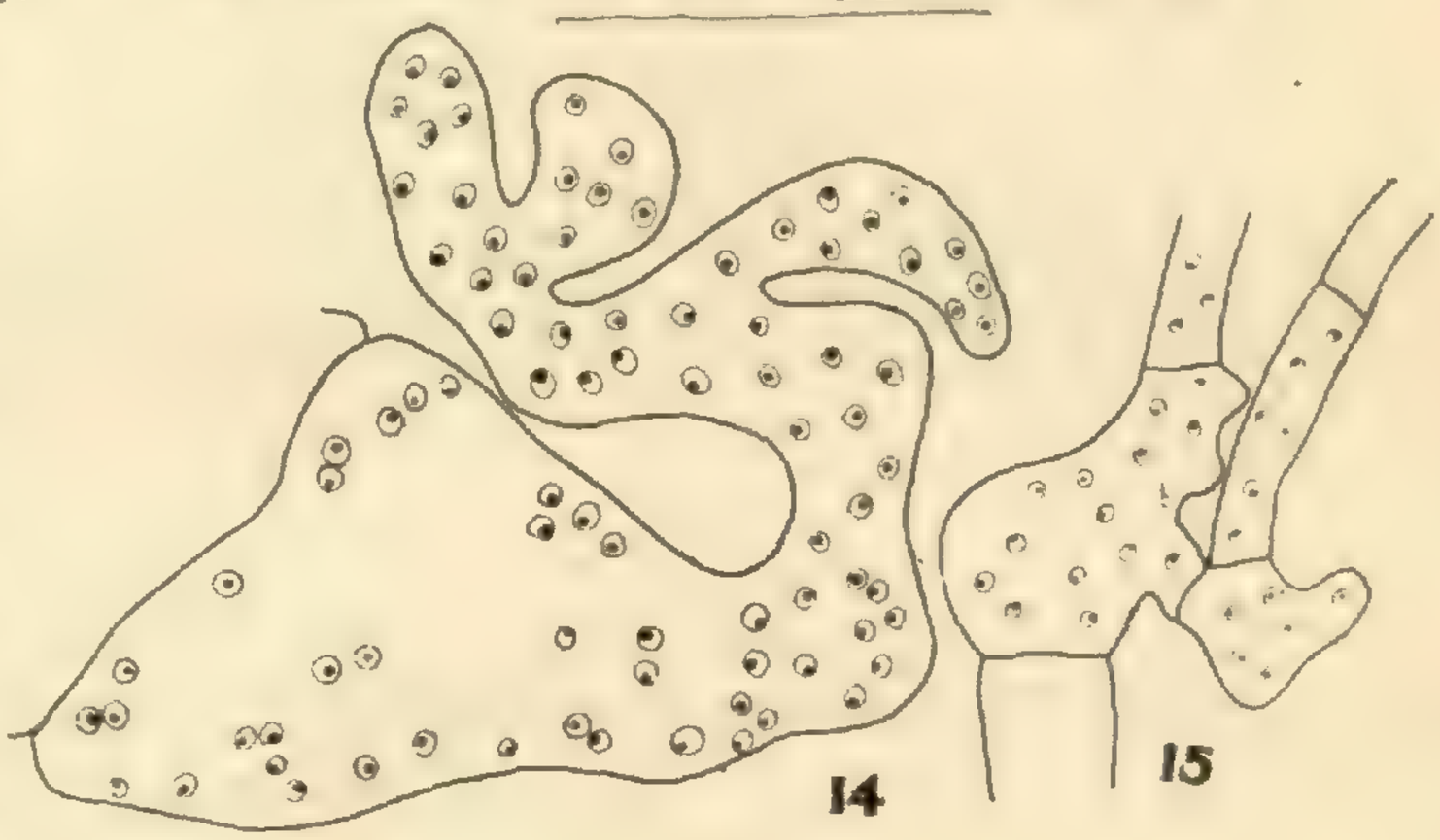
ever, the daughter nuclei reorganize so close together that after a slight growth they are pressed against each other and resemble fusing nuclei (fig. 13). The spindle fibers are frequently present at this stage, and can be seen connecting the two masses of chromatin, which are still visible in the daughter nuclei. Frequently the masses of chromatin lie against the nuclear membrane, and the disappearing fibers are entirely outside the nucleus, but at other times the fibers appear to cross the nuclear cavity, as in fig. 13. Frequently the chromatin appears, at first sight, to be in the center of the nucleus, when in reality it is lying against the membrane. This is due, of course, to the fact that the chromatin is at the upper or lower surface of the nucleus as it is viewed from above.

Division seems to take place rapidly throughout the growth of the ascogonium and the development of the ascogenous hyphae. The nuclei do not divide simultaneously, as all stages, including resting nuclei, can be found in a single ascogonium. There appear, however, to be periods in which division takes place, followed by others in which all of the nuclei are in the resting condition, for a large number of divisions are frequently found in a single ascogonium, while others show only resting nuclei. The same type of division that has just been described and the same number of chromosomes persist throughout the development of the ascogonium and ascogenous hyphae. The nuclei decrease somewhat in size during the growth of the ascogonium, and in the early stages of the development of the ascogenous hyphae, but as the ascogenous hyphae develop further, the nuclei increase in size until they come to be slightly larger than in the young ascogonium.

No fusion of nuclei has been observed in the ascogonium or in the ascogenous hyphae except in the tips where two nuclei fuse to form the primary nucleus of the ascus. A number of cases were seen in which two nuclei were pressed against each other, but in all of these the nuclear membrane was intact between the nuclei, and the appearance seemed to be due to the fact that the nuclei, after division, had reorganized close together, in the manner previously described. It may be said that a fusion of the nuclei would be hard to find, but they have been looked for very carefully in a large number of well fixed and stained preparations. The slight

decrease in the size of the nuclei during the development of the ascocarp and the persistence of the same number of chromosomes throughout the ascogonium and ascogenous hyphae, moreover, indicate very strongly that a fusion of nuclei during this stage is not to be expected.

When the ascogonium has reached its mature size, it gives off a number of large ascogenous hyphae which are multinucleate from the first (plate fig. 3). The nuclei do not appear to be arranged in pairs or in any other definite manner, but to be scattered irregularly in the hyphae (fig. 14). They are undergoing division rather rapidly, as has been previously described. About this time the cytoplasm and nuclei of the other cells of the archicarp begin to degenerate. These cells apparently do not fuse together as in *Ascophanus carneus* (CUTTING 7). The ascogenous hyphae grow up among the vegetative hyphae which are situated over the ascogonium and have been mentioned as giving rise to paraphyses. As the ascogenous hyphae increase in length, they branch freely and become divided up into a number of large multinucleate cells. Some nuclei are left in the ascogonium and these finally degenerate. When the ascogenous hyphae are growing out from the ascogonium, the vegetative cells over the ascogonium (plate fig. 3) are slender, densely protoplasmic, and extend upward toward the covering of the ascocarp. They thus have the appearance of young paraphyses, but do not take part in the formation of the hymenium until they have developed further. As they grow up they branch freely and



FIGS. 14–16.—Fig. 14, outgrowth of ascogenous hyphae from ascogonium; fig. 15, storage cells giving off paraphyses; fig. 16, tips of ascogenous hyphae in hymenium; all ×525.

become thicker and less densely protoplasmic. As the developing ascogenous hyphae grow up and branch among these vegetative hyphae, the older parts of the vegetative hyphae cease to have the appearance of paraphyses, while the younger parts still form a layer ahead of the ascogenous hyphae. When the place where the hymenium is to be formed is finally reached, the layer of paraphyses is thus already completely developed (plate fig. 4). The continued upward growth and branching of the vegetative and ascogenous hyphae causes the hymenium to have a much greater diameter than it would have had if it had been formed before the branching had taken place. Some of the vegetative hyphae in the subhymenial layer give off branches which form large, densely staining storage cells. These in turn give rise to more paraphyses (fig. 15). In a few cases nuclei in these storage cells have been seen to be fusing, and since in some cases the fusing nuclei are exceptionally large, it may be that nuclei which have been formed by fusion may themselves fuse. The fusion of nuclei in the storage cells is of regular occurrence in *Leotia* (BROWN **6**), but is probably exceptional in *Lachnea scutellata*, as most of the nuclei in the storage cells of this species are small and of nearly uniform size.

While the storage cells are being formed in the subhymenial layer, the ascogenous hyphae can be seen, in the same region, as rows of large multinucleate cells. These give off smaller multinucleate branches which extend upward into the lower part of the hymenium (fig. 16). It is from these branches that the asci are to be formed. The tips of these branches frequently contain two nuclei, and it seems probable that these are cut off together in a single cell, as no such uninucleate cells have been observed in the hymenium or subhymenial layer, although binucleate cells are of frequent occurrence. It is, of course, still possible that uninucleate cells may sometimes be cut off, and that these may have been overlooked, as the uninucleate condition would probably last only a short time. The cutting off of two nuclei in the tip of an ascogenous hypha has been described by MCCUBBIN (**28**) in *Helvella elastica*. The cutting off of two nuclei or a single one, which subsequently divided, in *Lachnea scutellata* would probably not have any effect on the further development, since, as has already been

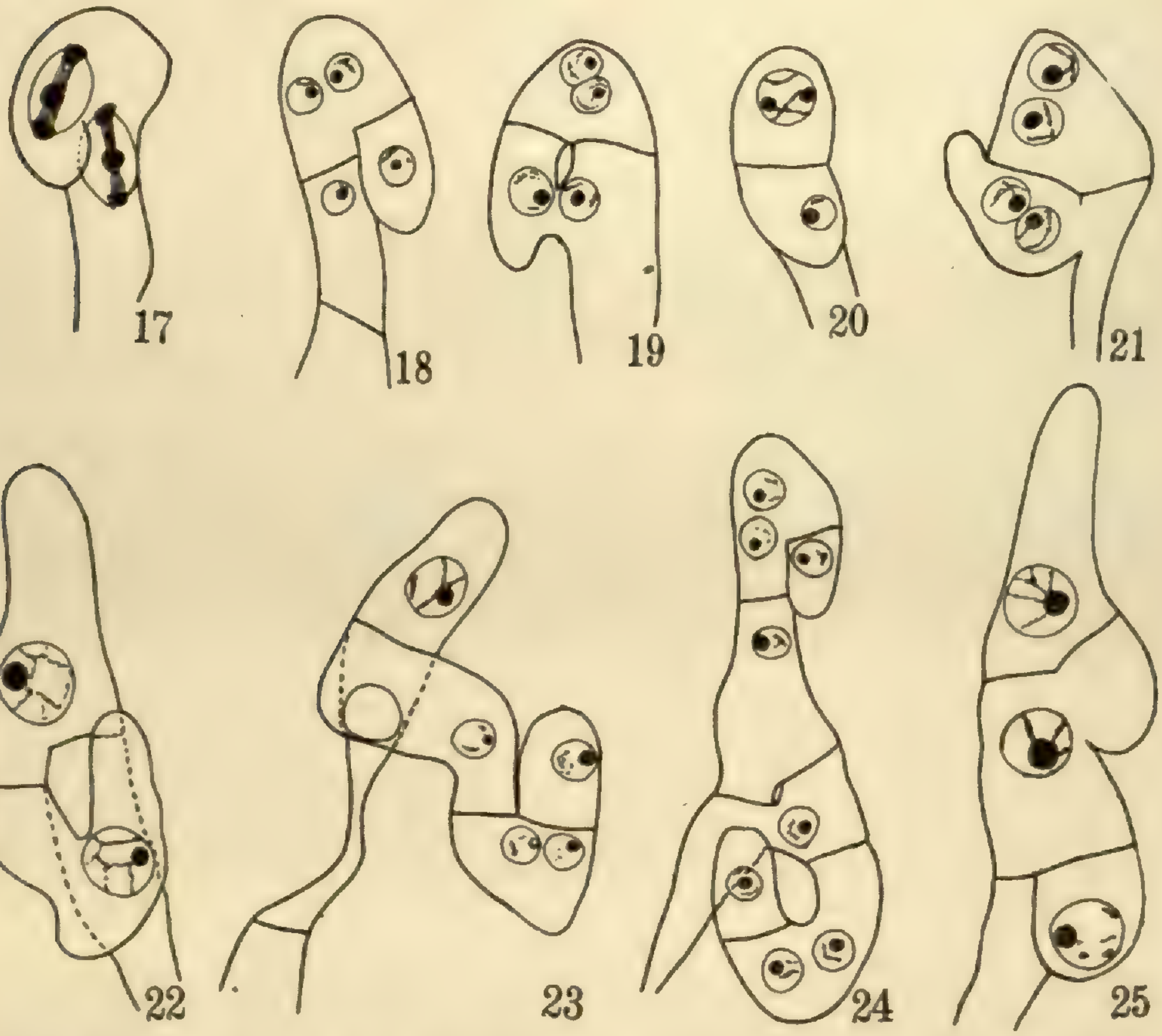
described, the nuclei undergo division in the ascogenous hyphae, so that the two nuclei which are in the tip of a hypha are probably closely related. There appears, moreover, as has been previously pointed out (BROWN **6**), to be no reason for thinking that the relation of fusing nuclei can make any difference, if these are all in the same plant and are derived from a single nucleus, with the haploid number of chromosomes.

The nuclei in those cells of the ascogenous hyphae which are below the hymenium finally degenerate. In doing so they often swell up to several times their original size, after which the nuclear membrane gradually disappears. This process is quite similar to that described by HARPER (**22**) for the nuclei in the trichogyne of *Pyronema confluens*. Before degenerating two or three of the nuclei sometimes fuse together. Such fusions are not confined to the nuclei of the ascogenous hyphae, but may occur in other degenerating cells.

The binucleate cells previously described as being formed from the ascogenous hyphae grow up in the hymenium and bend over at the tip. The two nuclei pass into the bent portion and divide in the same manner that has been described for the nuclei in the ascogonium (fig. 17). At metaphase there are five chromosomes, and at anaphase five pass to each pole. Walls come in between the daughter nuclei of each pair, thus forming a binucleate penultimate and a uninucleate ultimate and antipenultimate cell (fig. 18). This is of course a typical hook. The two nuclei in the penultimate cell may fuse to form the nucleus of an ascus (fig. 20), but often they divide and give rise to the nuclei of another hook (fig. 24). The ultimate cell usually grows down and fuses with the stalk (fig. 19), after which the nucleus from the stalk usually migrates into the ultimate cell (fig. 21), although occasionally the nucleus of the ultimate cell may pass into the stalk. After the nucleus of the stalk has migrated into the ultimate cell, it may fuse with the nucleus of the ultimate cell to form the primary nucleus of an ascus (fig. 22), but usually the two nuclei divide and the ultimate cell grows out to form another hook (figs. 23, 24). Sometimes the nucleus formed by the fusion of the nuclei of the ultimate and antepenultimate cells does not develop further. This is usually asso-

ciated with a vacuolated condition of the cytoplasm. Fig. 25 shows a case in which the penultimate cell has developed into a second hook. The nuclei of the ultimate and antepenultimate cells have fused, but the fusion nucleus has not developed further. The penultimate cell of the second hook has given rise to an ascus, while the nucleus of the ultimate cell has migrated into the antepenultimate and fused with its nucleus.

The processes described above, by which either the ultimate



FIGS. 17–25.—Fig. 17, tip of ascogenous hyphae, showing form of hook and division of nuclei; fig. 18, binucleate penultimate and uninucleate ultimate and antepenultimate cells; fig. 19, fusion of nuclei in penultimate cell and fusion of ultimate and antepenultimate cells; fig. 20, fusion nucleus in antepenultimate cell; fig. 21, migration of nucleus from antepenultimate to ultimate cell, followed by outgrowth of ultimate cell; fig. 22, formation of asci from both ultimate and antepenultimate cells; fig. 23, formation of hook from ultimate cell and ascus from penultimate; fig. 24, formation of hooks from both ultimate and penultimate cells; fig. 25, case in which nucleus from antepenultimate cell migrated into ultimate and fused with nucleus of ultimate; a hook was formed from binucleate penultimate cell, the penultimate cell of which in turn gave rise to an ascus, while the nucleus of the ultimate cell migrated into the antepenultimate and fused with its nucleus; all ×1400.

or antepenultimate cell may give rise to a hook, may be repeated many times, so that a large number of asci may be formed finally from a single hypha. Even in young ascocarps, five or six hooks may frequently be seen joined together in various ways, and if it were possible to follow a hypha for a considerable distance, the above number would of course be greatly increased.

The significance of these phenomena has been discussed in a previous paper on *Leotia* and *Geoglossum* (BROWN **6**), in which genera they also occur.

As new hooks are successively developed from older ones, that part of the ascogenous hypha which connects the successive hooks, as well as the older parts of the hypha, become vacuolated to such an extent that no cytoplasm can be seen in them. Despite this fact, new hooks and asci are formed quite rapidly. It seems probable, therefore, as HARPER (**22**) suggests, that the developing asci obtain their nutrient material from the paraphyses, which are in contact with them, by transfusion through the walls.

The multiplication of the number of hooks gradually raises the level at which asci are formed. At the same time, the level at which the paraphyses come off is also raised by the formation of new ones from the basal portion of older ones and from storage cells which are being continually formed at a higher level. As growth continues and the hymenium rises higher and higher, the subhymenial layer is increased in height by the addition of the older parts of the hymenium, which are gradually left behind.

While the hymenium is thus being raised, it also increases in diameter. As has already been described, the cells between the hymenium and cortex continually produce new cells which give rise to paraphyses around the margin of the hymenium. At the same time, hooks formed from the ultimate or penultimate cells of older ones grow in among the paraphyses. Owing to the processes described above, an ascocarp, after it assumes its mature form, may increase greatly in both height and diameter.

When the two nuclei which fuse to form the primary nucleus of the ascus are in the process of fusion, they contain comparatively little chromatin. This is scattered somewhat irregularly on linin fibers, but shows an approach to the spireme condition

(fig. 26). The fusion nucleus grows rather rapidly, and as this continues the chromatin soon comes to be arranged in a definite, fine spireme (fig. 27). When this condition has been reached, the spireme does not usually show any free ends, and it can frequently be traced as a continuous thread for considerable distances. It is impossible, however, to follow it through some of the tangles. Frequently threads run to the nuclear membrane or nucleolus, after which it is not possible to trace them further. This suggests that the spireme is not continuous throughout its entire length, but this conclusion must be considered doubtful, as it is difficult to follow a spireme along the nuclear membrane, which is usually irregularly thickened, or to distinguish it from the nucleolus when it is in contact with the latter. While the nucleus is still far from its final size, the spireme shows the approach of synizesis by beginning to collect in a tangle either around or to one side of the nucleolus (fig. 27). This usually continues until all of the spireme is arranged in a dense tangle in which little detail can be seen (fig. 29). No evidence of a fusion of spiremes during this stage was observed. An examination of figs. 27 and 28 will show that the spireme is not double as it goes into synizesis. The spireme was occasionally seen contracted into a mass about as dense as the nucleolus. This extreme condition may have been due to fixation, but the regular occurrence of synizesis at this stage, and in material in which the fixation seemed to be perfect, certainly seems to indicate that synizesis is, as MOTTIER (**29**) thinks, a stage in development, and not an artifact due to fixation, as is claimed by SCHAFFNER (**32**). This view is supported by the fact that the spireme is quite different in appearance before and after synizesis. Synizesis probably lasts for a considerable time, as the nucleus and ascus grow considerably during this period.

At the end of synizesis the spireme, which is now much thicker than before, loosens up and becomes spread through the nucleus (figs. 30 and 31). The continuity of the spireme throughout its length at this stage is, just as before synizesis, doubtful. After the spireme has become spread through the nucleus, it splits longitudinally (fig. 32). This splitting appears to extend through almost if not quite the entire length of the spireme. The two halves,

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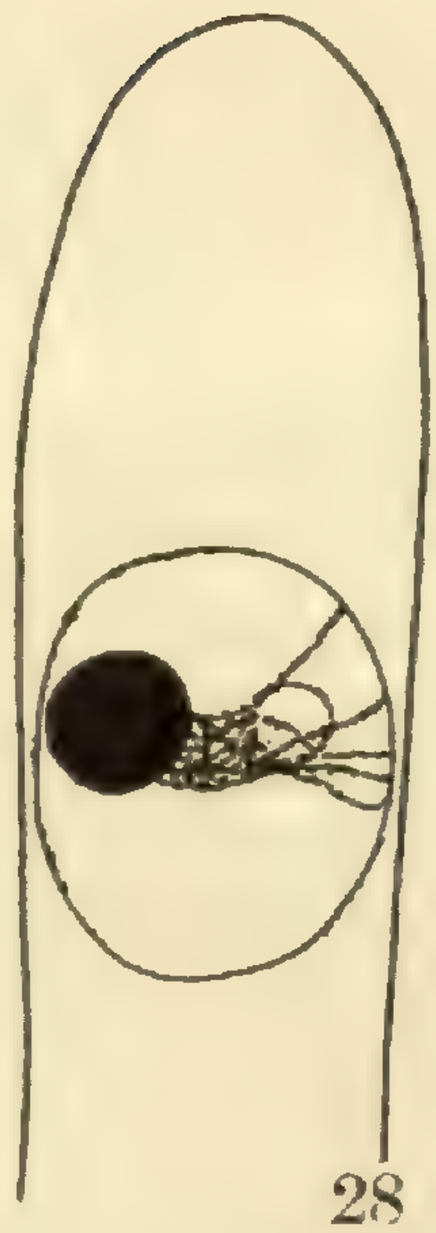

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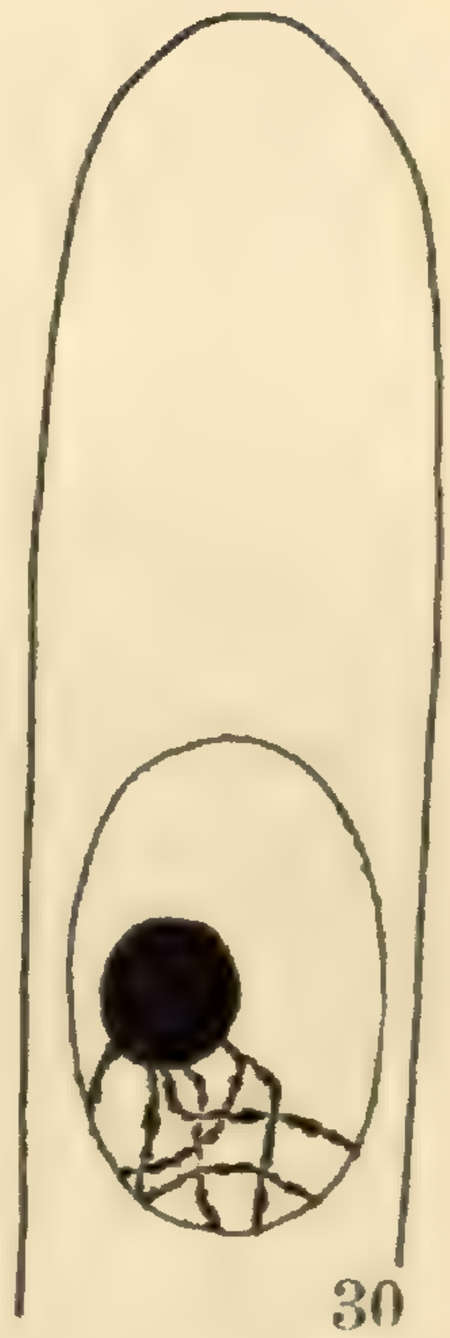

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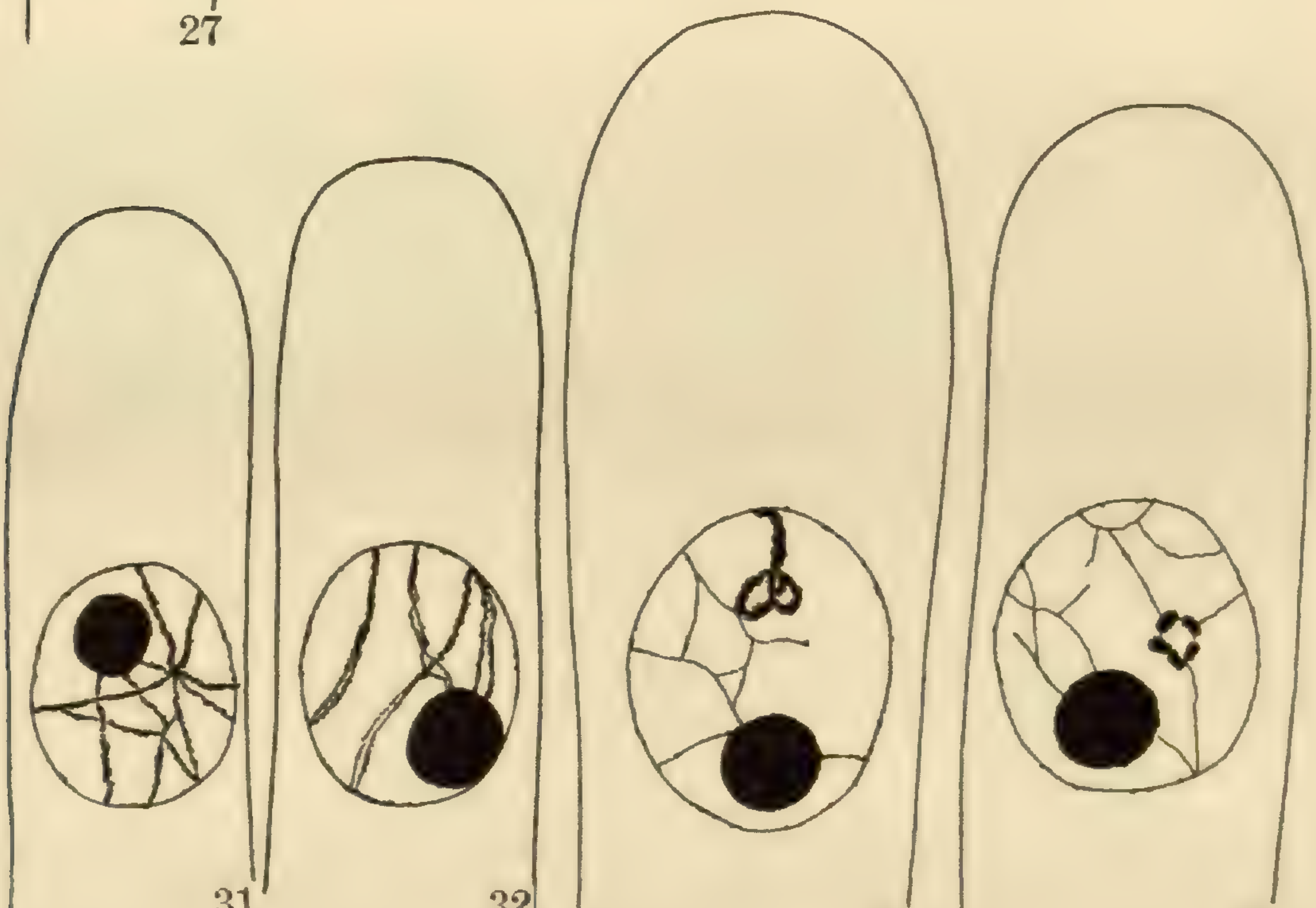

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FIGS. 26–34.—Fig. 26, fusion of two nuclei in ascus; fig. 27, early stage in approach of synizesis in nucleus of ascus; fig. 28, later stage in approach of synizesis; fig. 29, synizesis in nucleus of ascus; fig. 30, spireme just after synizesis; fig. 31, spireme spread through nucleus; fig. 32, split spireme; fig. 33, contracted spireme just before formation of chromosomes; linin fibers apparent; fig. 34, nucleus with five chromosomes and well developed fibers; all ×2800.

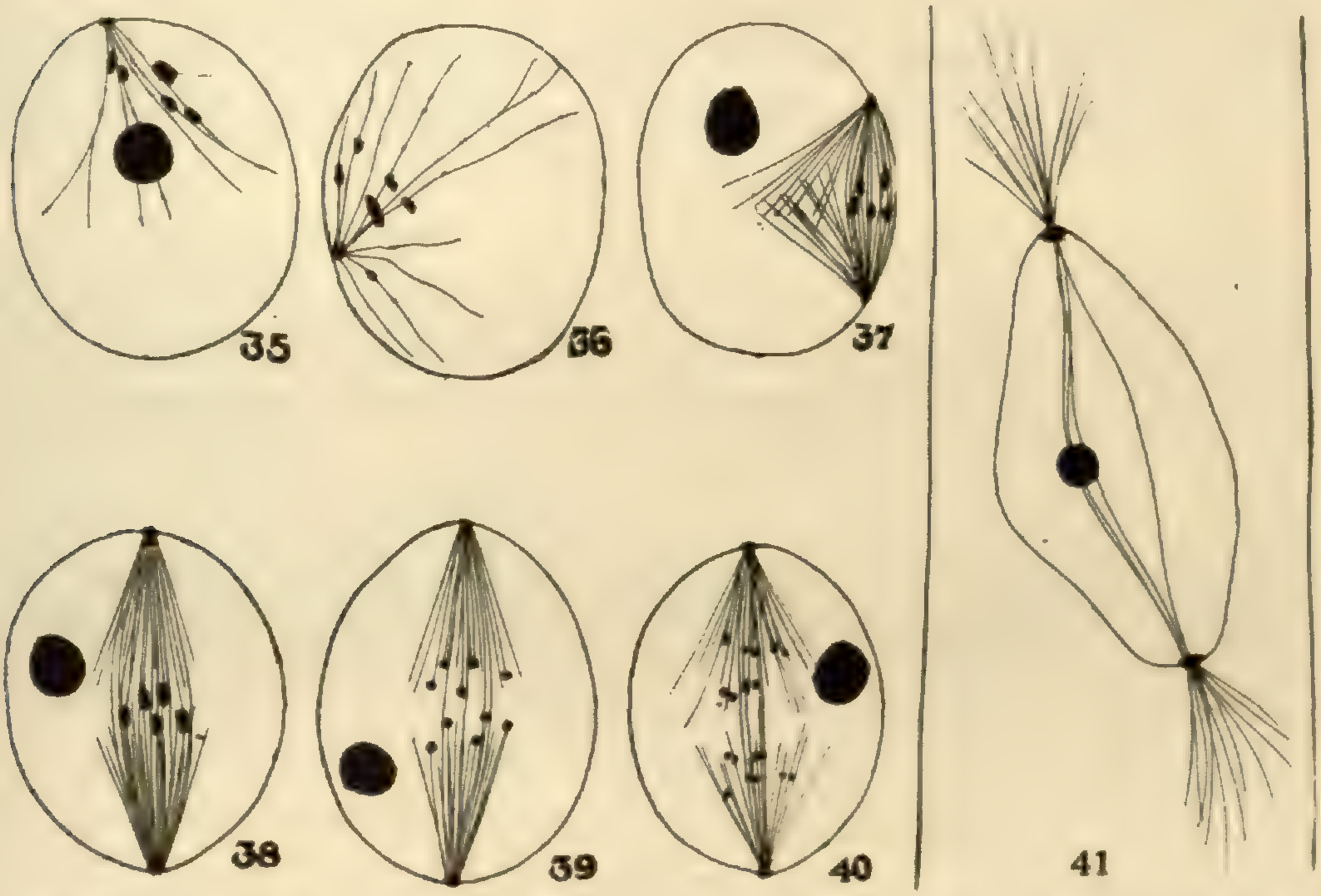
however, soon come together again, after which all traces of the split are usually lost, although sometimes evidences of it may be apparent even after the formation of the chromosomes.

After the two halves of the spireme have come together, it begins to contract. This contraction continues until the spireme shortens very considerably (fig. 33). The spireme at this stage has the appearance of a continuous thread, the ends of which are probably free. The spireme finally segments into five somewhat elongated chromosomes (fig. 34). Each of these chromosomes is probably bivalent, since the nucleus received five chromosomes from each of the two nuclei which by fusing gave rise to it. The bivalent condition, however, is not indicated by the form of the chromosomes. In this they are probably similar to those of most plants. In *Peperomia* (BROWN **4**), however, the two halves appear during the heterotypic prophase, as separate chromosomes connected by linin fibers; while in *Oenothera* (GATES **17**) the diploid number of chromosomes appears at the same stage, and in this case some of the chromosomes may not be arranged in pairs.

As the spireme contracts, linin fibers appear within the nucleus (fig. 33). Along those fibers, and especially in the early stages, there are small granules which have the appearance of chromatin. They usually stain less densely than the chromatin of the spireme, but frequently they are large and numerous enough to make the fibers along which they are scattered resemble the spireme. It was not possible to tell whether the substance of these granules passed to the chromosomes or took part in the formation of more linin fibers, but since as they disappear the number of linin fibers increases considerably, it seems probable that part of the granules take part in the formation of the fibers. No evidence of the formation of these fibers from the linin of the spireme by the migration of the chromatin has been observed, but since the continuity of the spireme in the early stages is doubtful, and these fibers may resemble the spireme very closely, such a possibility, while not probable, can hardly be said to be excluded. It is certain, however, that most of these fibers which will later on take part in the formation of the spindle are formed *de novo*.

As the spindle fibers increase in number, they become connected

with a centrosome which makes its appearance on the nuclear membrane, and some of them connect the centrosome with the chromosomes (fig. 35). No signs of this centrosome have been visible up to this time, and as there is nothing to indicate that it persists through the resting stages, it is probable that it is formed *de novo* at each division. In this respect it resembles the centrosphere-like bodies in *Polysiphonia violacea* (YAMANOUCHI **39**), the centrospheres in *Corallina* (DAVIS **11**), and the kinoplasmic caps in *Griffithsia bornetiana* (LEWIS **25**). Deeply staining granules are frequently present in the cytoplasm of *Lachnea*. These are particularly abundant around the nucleus at this division. The nuclear membrane does not have an even appearance, but is irregularly thick, and often the granules just described are in contact with it. Owing to these facts it has not been possible to trace the origin of the centrosome. The centrosome here, as in the divisions previously described, is not a spherical body, but a flattened structure composed of a number of granules.



FIGS. 35–41.—Fig. 35, fibers attached to centrosome; fig. 36, nucleus showing extra body which appears much like a chromosome; fig. 37, late prophase of first division in ascus; fig. 38, metaphase of first division; fig. 39, early anaphase of first division; fig. 40, late anaphase, showing division of daughter chromosomes; fig. 41 telophase of first division; all ×2800.

When the five chromosomes have become connected with the centrosome, other deeply staining bodies are frequently present on the linin fibers. These are usually small and are probably similar to the granules previously described. Sometimes, however, they are as large as or larger than the chromosomes, and may bear such a striking likeness to them that there may appear to be as many as six or seven chromosomes (fig. 36). When the spindle is completely formed, these bodies may still be present on fibers connected with the spindle or nucleolus. Only very small ones, however, have been seen on the spindle, so that when the spindle is formed these bodies, which usually stain lighter than the chromosomes, can be readily distinguished from them.

After the linin fibers have become connected with the centrosome, they increase in number. The centrosome then divides, and the two daughter centrosomes take positions at the opposite ends of the spindle (figs. 37 and 38). When the spindle is first formed, it may be at any angle to the longitudinal axis of the ascus, but as division proceeds, it takes a position which is approximately parallel to it. While this is taking place, a set of fibers makes its appearance outside the nucleus. These fibers radiate from the centrosome into the cytoplasm for a considerable distance.

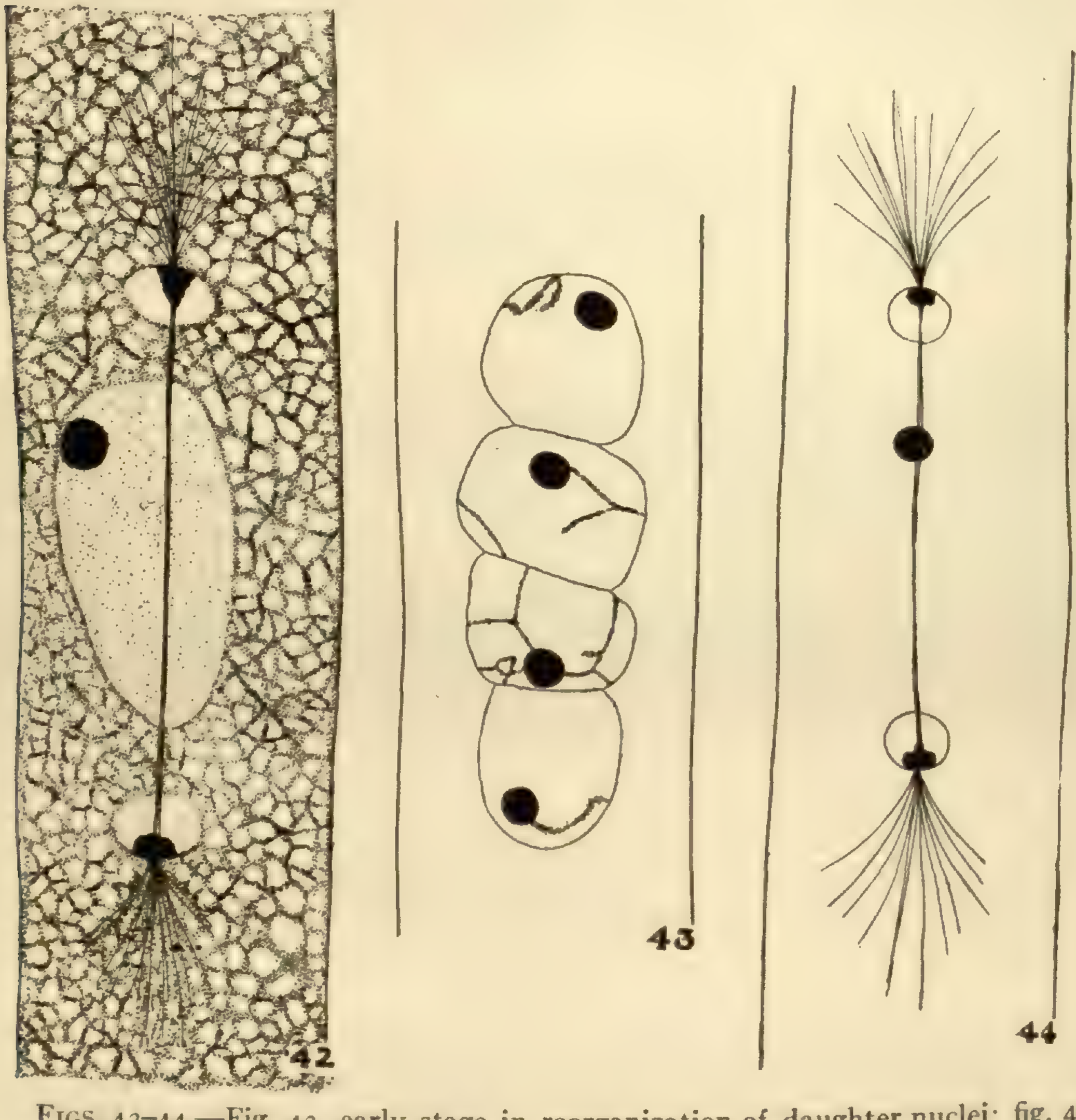
At metaphase five chromosomes are present on the spindle (fig. 38). Usually all of these appear to be somewhat elongated and have their longitudinal axis parallel to that of the spindle. Each of the five chromosomes divides transversely, but the divisions do not all take place at the same time, so that as division proceeds, anywhere from six to ten chromosomes may be counted on the spindle. Remembering that when the spireme segmented it gave rise to five elongated chromosomes which were probably bivalent, it would seem that this division probably separates chromosomes which were placed end to end on the spireme and can have nothing to do with the longitudinal split seen in the prophase. There appears to be nothing to indicate that the chromosomes which went into the fusion nucleus have persisted unchanged through the resting nucleus and the prophases of this division, and are the same as the chromosomes which are separated at metaphase. On the contrary, there would seem to have been every chance for an

exchange of material during synizesis, if not during the resting stage. The independence of unit characters in heredity would seem to favor the view that there may be an exchange of material between chromosomes, for if a given set of unit characters were permanently associated with the same chromosomes, we would expect to find different characters correlated much oftener than they are. If, however, as is generally assumed, the chromosomes are the part of an organism which is responsible for the transmission of hereditary characters, and if different chromosomes are not alike but responsible for different characters, it would be impossible for a promiscuous exchange of material between various chromosomes to occur without producing chaos. It would seem more likely that the chromosomes are so constituted that only certain kinds of material can be fitted into them, so that while chromosomes derived from different nuclei may exchange material which is responsible for similar sets of characters, they cannot exchange material which is responsible for one kind of character for that responsible for a different kind.

The chromosomes at the first division in *Lachnea* appear to approach the poles rather slowly, as anaphase is very abundant in sections. The ten chromosomes, formed by the division of the five seen at metaphase, are at first grouped at the equator of the spindle and give this stage a striking resemblance to metaphase. Finally, however, they separate into two groups of five, one of which goes to each pole (fig. 39). As the chromosomes approach the poles all of them may again divide (fig. 40). The two halves of a chromosome do not appear to be connected, but when division has just taken place the halves appear to be arranged in pairs, the constituents of which usually lie side by side on the spindle. It would seem from this that this division is due to a longitudinal splitting, and this may be connected with the splitting of the spireme seen in the prophase. A division of the daughter chromosomes as they approach the poles has been described in *Gallactinia succosa* by MAIRE (**27**) and GUILLIERMOND (**18**).

After the chromosomes have reached the poles, the fibers which connect the centrosomes continue to elongate until they become markedly bent. At the same time, breaks are formed on the

nucleus at each pole (fig. 41). Finally the groups of chromosomes break through the nuclear membrane, after which the fibers which connect the chromosomes straighten out and the groups of chromosomes are carried far beyond the limits of the nucleus (fig. 42). The nuclear membrane then breaks down. The nucleolus is left



FIGS. 42–44.—Fig. 42, early stage in reorganization of daughter nuclei; fig. 43, four nuclei of an ascus in contact; fig. 44, late stage in reorganization of daughter nuclei after first division; all ×2800.

in the cytoplasm and finally disappears. Both the fibers which connect the centrosomes and those which radiate out into the cytoplasm frequently persist until after nuclear membranes have been formed around the daughter nuclei (fig. 45). Sometimes the groups of chromosomes are not separated so far, and in this case the daughter nuclei may reorganize in contact with each other.

Occasionally this may occur at both the first and second divisions (fig. 43).

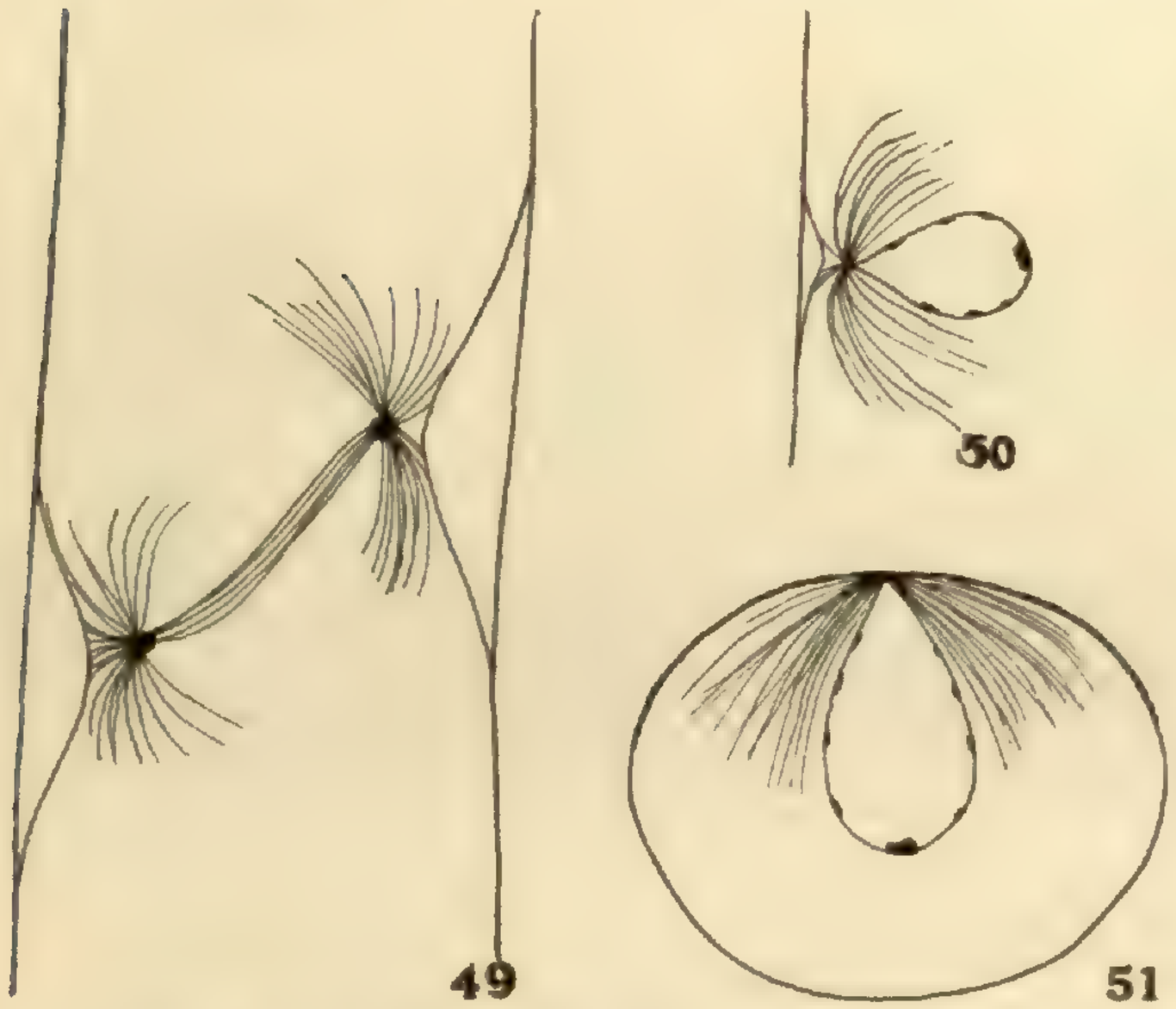
When the two groups of chromosomes have reached the place where the daughter nuclei are to be reorganized, they lie at the ends of the fibers which connect the centrosomes and just below those which radiate out into the cytoplasm. A clear area then makes its appearance on the side of the chromosomes which is away from the radiating fibers (fig. 42), and a membrane is formed around this clear area (fig. 44). The centrosome appears to be on the nuclear membrane and can be distinguished until the nucleus grows considerably, but after a time it seems to disappear. When the nucleus is first formed, the chromosomes are still arranged in a group on that side of the nucleus which is near the radiating fibers. As growth proceeds this group gradually grows smaller, while masses of chromatin make their appearance on other parts of the nuclear membrane. The nuclei are usually pear shaped (fig. 45). This appearance suggests that the radiating fibers exert a pull on the nucleus.

FIGS. 45–48.—Fig. 45, daughter nuclei reorganized; fig. 46, resting nucleus between first and second divisions; fig. 47, metaphase of second division; fig. 48, anaphase of second division; all ×2800.

The next division is homotypic, and shows no new features. The chromatin becomes arranged in a spireme (fig. 46) which gives rise to five chromosomes. These chromosomes are usually rather close together, and frequently they become aggregated in a rather dense mass. This phenomenon appears to be similar to the grouping of the chromosomes in the prophases of the divisions in

the ascogonium and ascogenous hyphae. The spindles of this division are similar to those of the first, and usually lie in a plane which is approximately parallel to the axis of the ascus, but, as HARPER (**21**) has shown, they may vary markedly from this position. At metaphase the five chromosomes divide and five pass to each pole. Telophase and the reorganization of the daughter nuclei appear to be entirely similar to the same processes as described at the end of the first division.

The third division is essentially like the second, except that the spindles are usually approximately at right angles to the axis of the ascus although, as HARPER (**21**) has shown, one of them may be parallel to the ascus wall. At telophase, when the masses of chromosomes have broken through the nuclear membrane, some of the fibers which radiate from the centrosome out into the cytoplasm appear to be connected to the plasma membrane around the ascus (fig. 49). Where this occurs, the plasma membrane is pulled in toward the groups of chromosomes as though the fibers which connect the groups of chromosomes with the plasma membrane, by contracting, were drawing the membrane and group of chromosomes together (fig. 49). As the groups of chromosomes approach the periphery of the ascus, the radiating fibers come to be bent backward; this may be due to the movement of the centrosomes. The nuclei reorganize in a manner similar to that described for the daughter nuclei at the end of the first division, except that a more pronounced beak is formed on the nucleus where the radiating fibers



FIGS. 49–51.—Telophase of third division; radiating fibers attached to plasma membrane; fig. 50, nucleus reorganized after third division; fig. 51, spore showing beginning of secondary thickening of wall; fibers still apparent; all ×2800.

are joined to the centrosomes (fig. 50). The plasma membrane around the ascus, which was pulled in where the radiating fibers were connected with it, has by this time very nearly resumed its normal position against the ascus wall (fig. 50). The nucleus which is still connected by fibers to the membrane is, by this means, drawn toward the periphery, and this may account for the beak and also for the further bending back which has taken place in the radiating fibers which were not connected with the membrane.

Since the fibers seem to exert a pull on both the plasma membrane and the nucleus, and to be bent as a result of the movement of the nucleus, it would seem that they must be relatively solid structures. This view is strengthened by their behavior during telophase in all three divisions. After the chromosomes have reached the poles, the fibers connecting the centrosomes continue to grow and become bent as though under tension. At the same time beaks are formed on the nuclei at both poles. This may be due to the pressure of the connecting fibers, or in part at least to a pull exerted by the fibers radiating into the cytoplasm, as in the case of the beaks formed on the eight nuclei.

HARPER (**19, 21, 22, 23**) has described the cutting out of the spores in *Erysiphe*, *Lachnea scutellata*, *Pyronema*, and *Phyllactinia*. According to this author, the fibers radiating into the cytoplasm fold back and fuse into a membrane which grows back until its edges meet at a point opposite the centrosome. FAULL (**12**) has studied spore formation in a number of Ascomycetes, and concludes that the spores are not cut out by a membrane formed of fused astral rays. According to him the spores are delimited by a limiting layer of protoplasm. On the site of this there is formed a plasma membrane about the spore, and another opposed to it lining the cavity in the epiplasm. The formation of these is probably preceded by a cleavage of the limiting layer. The exospore is formed between the two opposed plasma membranes. OVERTON (**31**) in *Thecotheus pelletieri* and FRASER (**14**) in *Humaria rutilans* describe the spores as delimited by the astral rays. In *Lachnea*, the first sign of the cutting out of the spore is the appearance of a delicate membrane at the outer limits of the recurved astral rays. This usually appears first around the centrosome

and then is formed progressively until it cuts out the spore. This membrane is apparently not formed by a fusion of the astral rays, for although it appears at their outer limit, after it is completely formed the rays are still present within the spore and are apparently as numerous as ever, and in shrunken material both the centrosome and astral rays may be drawn completely away from the spore membrane. Moreover, in *Lachnea* there do not appear to be enough fibers to fuse together to form a membrane, unless, as pointed out by FAULL (**12**), they become flattened out very considerably, and there is no evidence that such is the case. Where there are a large number of fibers, as in *Phyllactinia* (HARPER **23**), the fusion would be a much simpler matter, but that they are very numerous where the membrane appears, and disappear as it is formed, is not sufficient evidence that they fuse. It would be necessary to see the actual fusion to prove that the spore is cut out by a membrane formed of fused fibers. What part, if any, the centrosome and fibers take in the formation of the membrane is doubtful. The appearance of the membrane just outside of them suggests that they may have something to do with its position. On the other hand, sometimes even before the membrane is completely formed the centrosome may be within it and not in contact with it. Stages showing a spore partly cut out are relatively rare, which indicates that when the process is once begun it takes place rapidly. Miss FRASER (**14**) says that FAULL'S account of the cutting out of the spores "does not seem to satisfactorily explain either the persistence of the astral rays or the formation of the nuclear beak." In this connection it may be noted that in *Lachnea* the astral rays usually persist after both the first and second division, until the daughter nuclei are completely reorganized, and that beaks are frequently formed on the nuclei, although these are not so prominent as those on the nuclei of the spores.

During the early stages of the formation of the membrane, it appears to be simply a differentiated part of the cytoplasm, and it is difficult to determine exactly when a distinct wall is formed, but the wall appears to be produced on the site of the original membrane. After the wall has been formed around the spore, it begins to thicken (fig. 51). This process frequently commences in the

region around the centrosome, but it may begin at any point. After the wall has become thickened, it is easy to determine that it is a distinct wall, with plasma membranes on both sides of it. This is shown especially clearly in material which has been shrunken, when it is possible to find, side by side, cases in which all of the contents have a normal position, and others in which either the plasma membrane around the spore or the one lining the epiplasm is drawn away from the wall. At this stage the astral rays are still plainly visible.

The stage at which the nucleus retracts its beak and rounds up is somewhat variable, but it usually does not take place until after the formation of the wall. When the beak is withdrawn, the centrosome may be left in the cytoplasm, but more frequently it remains in contact with the nuclear membrane. In either case it finally disappears.

As the spore reaches its mature size the wall around it thickens and becomes the exospore.

Discussion

HETEROTYPIC MITOSIS

The method of reduction in the number of chromosomes in *Lachnea* is quite similar to that described in *Dictyota* (WILLIAMS **37**), *Fucus* (YAMANOUCHI **41**), and in a large number of the higher plants. The chromosomes are arranged end to end in the prophase of the heterotypic division, and there is no evidence of a parallel fusion of spiremes.

The reducing divisions in *Lachnea* are quite unlike those in *Phyllactinia* (HARPER **23**). This is perhaps not surprising in view of the great dissimilarity which, according to the work of DAVIS (**11**), YAMANOUCHI (**39**), and LEWIS (**25**), is shown by different genera of the Rhodophyceae. The great difference between the mitoses in *Lachnea* and *Phyllactinia* would certainly make it unsafe to carry any conclusions in regard to nuclear phenomena from one form to the other.

There is in *Lachnea* nothing resembling the double reduction described in some other Pezizineae by FRASER (**14**), FRASER and

WELLSFORD (**15**), and FRASER and BROOKS (**16**). This is in harmony with the view that there is no fusion in the ascogonium.

SEXUALITY

It is unnecessary to review here the history of our knowledge of the sexuality of the Ascomycetes, as this has been thoroughly done quite recently by HARPER (**22, 23**), OVERTON (**31**), and LOTSY (**26**); while the latest literature has been discussed by FRASER (**16**). The passage of the nuclei from the antheridium into the ascogonium of *Pyronema confluens*, as reported by HARPER (**22**) and confirmed by CLAUSSEN (**8**), would seem to have established the view that the antheridium and ascogonium are to be regarded as sexual organs, even though the antheridium may be functionless or lacking in other cases. DANGEARD'S (**10**) failure to find a passage of nuclei from the antheridium into the ascogonium of *Pyronema confluens* may be due, as BLACKMAN and FRASER (**3**) suggest, to his having worked on a different form from that observed by HARPER and CLAUSSEN. The writer has found that the antheridia may behave differently in different strains of *Pyronema confluens*. In one (BROWN **5**), the antheridia never fused with the trichogyne, while in a strain of *Pyronema* (*confluens*) *omphalodes*, obtained through the kindness of Dr. F. J. SEAVER, the antheridium at the proper stage, as has been figured by him (SEAVER **34**), can be readily seen fused to the trichogyne. The two strains, moreover, show differences in the conditions under which they can be grown. It is interesting in this connection that VAN TIEGHEM (**35**) has shown that under cultural conditions the antheridium of *Pyronema confluens* may be normal, rudimentary, or absent, while the ascogonium develops normally.

Since recent work has shown that the fusion of nuclei is the essential part of fertilization, the discussion of the sexuality of the Ascomycetes has naturally centered around the nuclear fusions. In the simple forms *Eremascus fertilis*, *Endomyces magnusii* (GUILLIERMOND **18**), and *Dipodascus albidus* (JUEL **24**), the antheridium and oogonium fuse and give rise at once to a single ascus. In *Eremascus fertilis* the antheridium and oogonium are uninucleate, and in all three cases the primary nucleus of the

ascus is formed by the fusion of a nucleus from the oogonium and one from the antheridium.

Among the Erysibaceae, HARPER (**19, 20, 23**) has described the fusion of a uninucleate antheridium and oogonium in *Sphaerotheca humuli*, *Erysiphe communis*, and *Phyllactinia corylea*. According to HARPER, the male and female nuclei fuse in the oogonium, and this is followed later by a second nuclear fusion in the ascus. DANGEARD (**9, 10**) has studied the development of *Sphaerotheca humuli* and *Erysiphe*, and denies the presence of a fusion in the oogonium.

BARKER (**2**) has described the fusion of an antheridium and oogonium in *Monascus*. He did not find a fusion of nuclei in the oogonium, but attributed this to his failure to get the proper stages. SCHIKORRA (**33**) has also described the fusion of an antheridium and oogonium in *Monascus*, but does not find any fusion of nuclei except the one in the ascus.

Among the Pezizineae the fusion of nuclei in pairs in the ascogonium has been described in *Pyronema confluens* (HARPER **22**), *Humaria granulata* (BLACKMAN and FRASER **3**), *Lachnea stercorea* (FRASER **13**), *Ascobolus furfuraceus* (WELLSFORD **36**), *Ascophanus carneus* (CUTTING **7**), and in the vegetative hyphae in *Humaria rutilans* (FRASER **14**). In all of the above cases a second fusion is described in the ascus. CLAUSSEN (**8**), however, after studying *Pyronema confluens*, has concluded that there was no fusion of nuclei in the ascogonium. BROWN (**4**) came to the same conclusion in regard to a form of this species in which the antheridium did not fuse with the trichogyne. This conclusion was confirmed by the behavior of the chromosomes in the ascus. In *Lachnea* it would seem to be quite evident that there is no fusion of nuclei in the ascogonium, but there are appearances connected with division which may be readily mistaken for fusions. During prophase, when the nuclei are of course large, the massing of the chromosomes into a nucleolus-like group gives an appearance much like a fusion nucleus, while the reorganization of fusing nuclei in contact simulates fusing nuclei rather closely. Similar appearances have been seen by the writer (BROWN **4**) in *Pyronema*. In view of these facts and the increasing amount of negative evidence, it would

seem necessary to study the structure and behavior of the nuclei in the ascogonium quite closely before deciding that there is a fusion of nuclei in the ascogonium of any of the Pezizineae, and it is worthy of note that divisions have not been described in any of those mentioned above in which such a fusion is said to occur. This is particularly true of such an aberrant case as the occurrence of a second fusion following the sexual one in the life history of the same plant.

ALTERNATION OF GENERATIONS

When HOFMEISTER used the term alternation of generations, he of course did not know of the alternation of the haploid and diploid number of chromosomes, but meant the alternation of two kinds of plants, one of which bore sexual and the other asexual reproductive bodies. Since the significance of nuclear phenomena has come to be better understood, many writers have been inclined to use the term alternation of generations as synonymous with the alternation of the haploid and diploid number of chromosomes, but the question may be asked as to whether the two things always necessarily coincide. If we take the cases of *Alchemilla* (MURBECK **30**), which has an embryo sac with the diploid number of chromosomes, and *Nephrodium* (YAMANOUCHI **40**), which produces sporophytes with the haploid number, there is of course no alternation of the haploid and diploid number of chromosomes, but from the standpoint of phylogeny there is an alternation of two kinds of plants. In *Coleochaete*, where the zygospore divides to form a number of cells which produce zoospores, the cells formed from the zygospore may be regarded as an intercalated asexual phase, but reduction takes place at the first division of the zygospore (ALLEN **1**). Here there would seem to be, as FARMER has suggested, a sporophyte which normally has the same number of chromosomes as the gametophyte. In the red alga *Griffithsia bornetiana*, LEWIS (**25**) thinks that the sexual plants and the mass of carpospores constitute an antithetic alternation of generations, while the sexual and tetrasporic plants represent the alternation of an homologous phase. According to this interpretation, the diploid number of chromosomes would extend through two distinct phases.

It seems probable that the ascogonium in some of the ancestors of *Lachnea scutellata* was fertilized, and that this ended the gametophytic phase and initiated the sporophytic, which ended in the production of spores. According to the interpretation usually applied to the delayed nuclear fusion in the rusts, the above interpretation would hold even if nuclear fusion was delayed, as CLAUSSEN (8) claims to be the case in *Pyronema confluens*, until the formation of the ascus.

From a phylogenetic standpoint, it would seem reasonable, therefore, in the case of *Lachnea scutellata* to regard the stages from the spore to the ascogonium as gametophytic, and those from the formation of the ascogenous hyphae to the production of spores as sporophytic. The diploid number of chromosomes exists, however, only in primary nucleus of the ascus. Even if we should adopt DANGEARD'S (10) interpretation, and regard the ascus as an oogonium, the third division in the ascus, which shows the haploid number of chromosomes, would still appear to belong to the sporophyte. It would seem advisable, therefore, in the case of *Lachnea scutellata*, as in those previously mentioned, to distinguish between the alternation of generations and the alternation of the haploid and diploid number of chromosomes. The gametophyte is usually regarded as beginning with the spore mother cell, but if the ideas brought forward here are correct, this can hardly be the case in *Coleochaete* or *Lachnea scutellata*, and it would seem better to think of it as beginning with the spore.

Summary

The mature ascocarp of *Lachnea* is disk-shaped. The hymenium forms the upper surface, while the rim and lower surface are covered by a thick-walled cortical layer. The center is composed of rather loosely interlacing hyphae.

The ascogonium is the penultimate cell of a row of about nine.

The ascogonium is early surrounded by vegetative hyphae, the outer of which form the first part of the cortex, while those around the ascogonium remain active and give rise on one side to more of the cortex and on the other to hyphae which will produce paraphyses. When a part of the cortex is once formed, the develop-

ment of the hyphae composing that part ceases. The cells between the cortex and hymenium, however, remain active and add to the cortex and to the hyphae which produce paraphyses.

The ascogenous hyphae are large and branch profusely. At the ends of these are formed typical hooks, consisting of binucleate penultimate and uninucleate ultimate and antepenultimate cells. The two nuclei of a penultimate cell may fuse to form the nucleus of an ascus, or they may divide and give rise to the four nuclei of another hook. The uninucleate ultimate cell usually grows down and fuses with the antepenultimate cell, after which the two nuclei may give rise to the nuclei of another hook, or they may fuse to form an ascus.

When the hymenium is first formed, it is covered by the younger setae of the cortex, but as its diameter is increased and its level raised by the multiplication of the number of asci and paraphyses, it comes to be exposed.

No fusion of nuclei was observed in either the ascogonium or ascogenous hyphae, except where two nuclei fuse to form the primary nucleus of an ascus.

The nuclei of the ascogonium and ascogenous hyphae appear to be entirely similar except for size, and the same number of chromosomes, five, persists throughout their divisions. When the chromosomes are first formed, they are frequently grouped in a mass resembling a second nucleolus. The chromosomes become connected with a centrosome which was not apparent during the resting stage. This centrosome divides, and the two daughter centrosomes come to be situated at the poles of the spindle. At metaphase the five chromosomes divide, and at anaphase five pass to each pole. The daughter nuclei are usually organized at some distance from each other, but sometimes they are so close together that they resemble fusing nuclei.

The first division in the ascus is heterotypic. Synizesis is produced by the contraction of a single spireme. After synizesis the spireme splits longitudinally. The two halves come together again, after which the spireme contracts considerably and segments into five elongated chromosomes. A centrosome makes its appearance on the nuclear membrane and becomes connected with the chromo-

somes by linin fibers in the nucleus. The centrosome divides and the daughter centrosomes come to be situated at the poles of the spindle. The chromosomes divide transversely. As they approach the poles they appear to split longitudinally. The second and third divisions in the ascus are similar to those in the ascogonium.

The spore wall does not appear to be formed by the fusion of astral rays.

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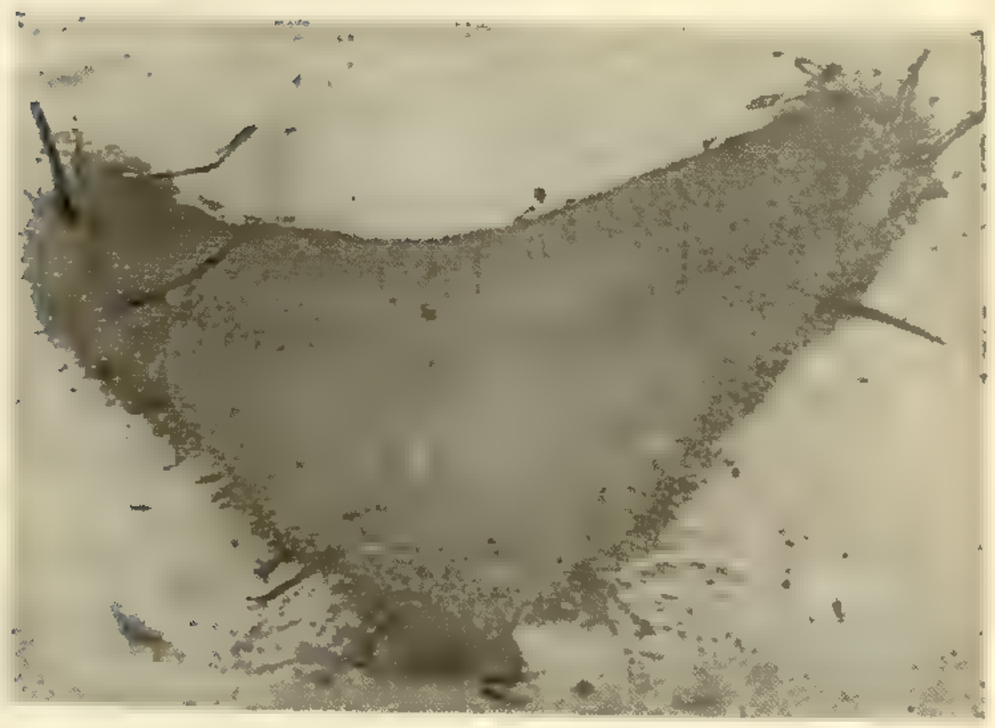

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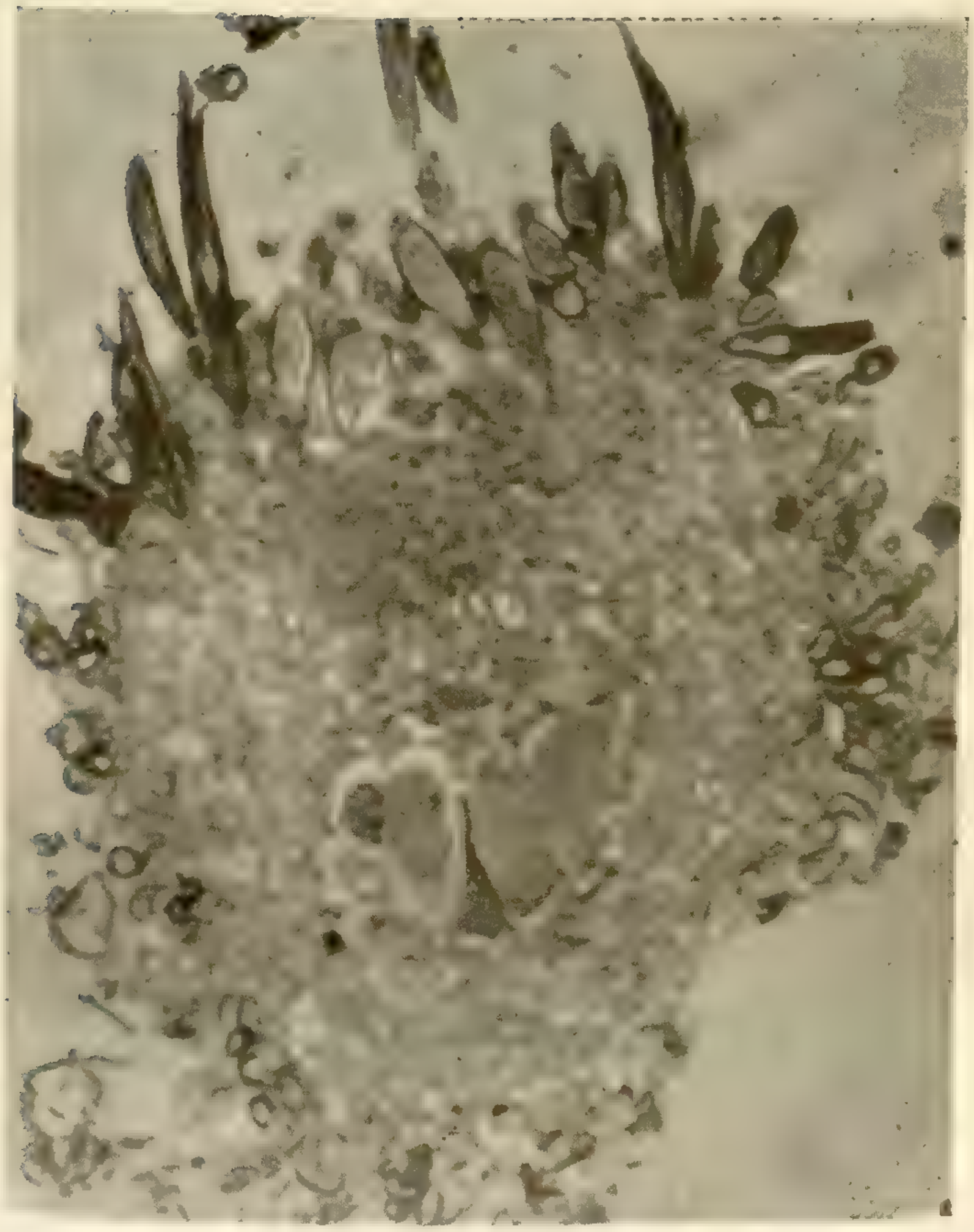

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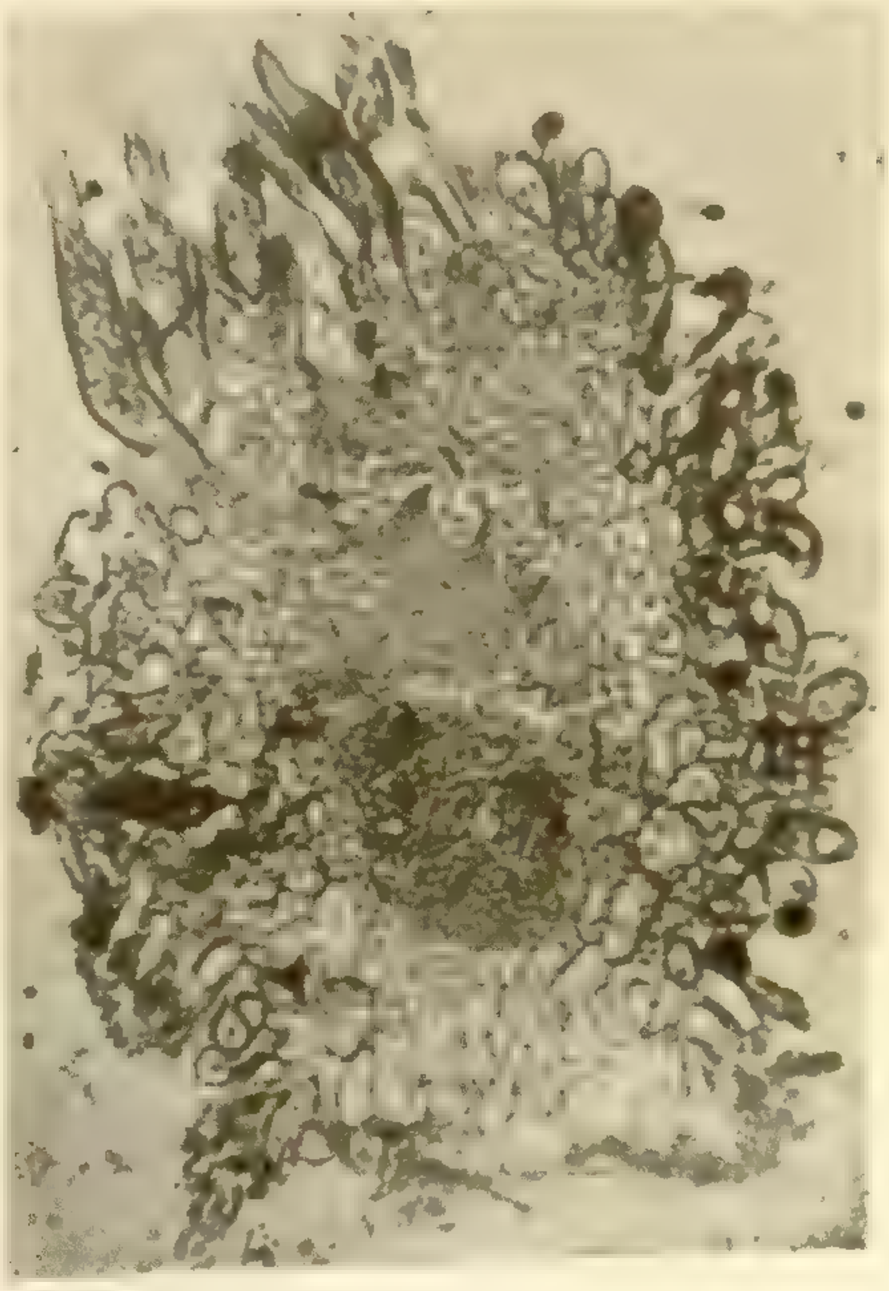

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EXPLANATION OF PLATE IX

FIG. 1.—Vertical section of mature ascocarp.

FIG. 2.—Vertical section of young ascocarp, showing young archicarp surrounded by comparatively few vegetative hyphae.

FIG. 3.—Vertical section of older ascocarp, showing ascogonium giving off ascogenous hyphae.

FIG. 4.—Vertical section of ascocarp, showing early stage in formation of hymenium.

PHYSIOLOGICAL BEHAVIOR OF ENZYMES AND CARBOHYDRATE TRANSFORMATIONS IN AFTER-RIPENING OF THE POTATO TUBER

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 148

CHARLES O. APPLEMAN

Introduction

An active growing period, followed by a period of rest, is a very general phenomenon among plants. Thus most seeds, tubers, and bulbs are structures whose growth processes have been arrested. Germination is simply a continuation of growth after the awakening from the rest period. The buds of the potato tuber, for example, will not grow, under the most favorable conditions, for several weeks after maturity; but after the awakening from this dormant condition they will grow under much less favorable conditions in a cold cellar.

Certain changes occur during the apparent dormancy, which are antecedent to the release of the growth processes, and these changes are known as "after-ripening." In many seeds the rest period is due to coat characters, which exclude or limit the supply of water or oxygen. After-ripening in such cases are processes which render the coats permeable to these substances. Often the processes of after-ripening are metabolic in character; this is especially true of tubers.

Certain external agencies artificially applied have been found to accelerate the processes of after-ripening, and thereby greatly shorten the natural rest period. MÜLLER-THURGAU (1) has shown that exposure to 0° C. for one month has this effect upon the resting potato tuber. Changes are thus brought about which break the rest period and allow growth to proceed several weeks earlier than under ordinary circumstances. He also found a great reduction of respiration, accompanied by an accumulation of sugars during exposure at low temperature.

The following work is a further study of the metabolic changes

occurring in the potato tuber as after-ripening proceeds during storage at 0° C. It is intended to throw some light upon the nature of the limiting factor or factors of growth during the rest period of this particular organ. Thus far a quantitative study has been made of digestive and respiratory enzyme changes and the carbohydrate food transformations.

Material

The material used for this investigation was the red land potatoes grown in Texas and procured only a few days after being harvested. This variety has a very short rest period. Two crops a year are grown in this climate, and samples from both crops were used in this work. The tubers were wrapped with paraffin paper and one-half stored at 0° C. and the remainder stored in a dark basement room at 20–25° C.

Methods

GLUCOSE, SUCROSE, AND STARCH.—The methods employed for the determinations of glucose, sucrose, and starch were virtually those of the association of official agricultural chemists (**7**). The glucose was determined according to the method of MUNSON and WALKER.

DIASTASE.—A modification of the starch iodine method (**8, 9**) was used in making the diastase determinations. One cc. of a 1 per cent soluble starch solution was placed in each of 10 test tubes surrounded with ice. Ascending amounts of the potato extract, prepared by grinding with quartz sand and filtering, were added to the tubes, beginning with 1 cc. and increasing the amount 0.1 cc. for each succeeding tube. The tubes were then incubated at 40° C. for 48 hours, placed again in ice, filled nearly full with water, and 3 drops of iodine solution added to each tube. The first tube in the descending series which showed a blue or violet color was considered the index for comparative diastatic activity. The method is impractical with larger amounts of extract on account of dark oxidation products and the precipitate which falls on addition of the iodine. If small amounts of both starch solution and extract are used, and the incubation continued for

48 hours, satisfactory duplicates may be obtained, so the method was considered sufficiently reliable for comparative purposes. A few drops of toluol were added to each tube during incubation, to insure against activity of bacteria.

CATALASE.—A detailed description of the method for the catalase determinations will be found in a recent paper by the author published in this journal (**4**). In all cases the water bath temperature was 25° C. during the experiment.

PEROXIDASE.—In order to compare the rate of peroxidase activity in the material under investigation, various methods were tried and variously modified. The methods differed mainly in the preparation and treatment of the extract, for in all cases guaiaconic acid was used as the oxidizable substance (**10, 11**). A definite quantity of extract was allowed to act upon a definite quantity of guaiaconic acid in the presence of hydrogen peroxide. The time required for the oxidation of the guaiaconic acid to reach a depth of blue equal to that of a standard tube, containing a solution of indigo carmine, was considered the index of the peroxidase activity. The standard tube was placed against a white background and screens arranged to eliminate shadows and unequal lighting. If the test tube is held against the standard tube, and the eye fixed upon the line separating the tubes, and the time noted when the color is the same on both sides of the line or when the line seems to disappear, quite accurate readings may be obtained with a little practice. The error of reading is greatly reduced if the test solution is of such dilution or the standard tube of such depth of blue that the time of reaction is not less than ten seconds nor greater than one minute. If the solution of indigo carmine is made up with pure distilled water, the fading of color at the end of several weeks is so slight that it falls well within the experimental error involved in comparing the shades of blue.

The present methods for peroxidase determinations are unsatisfactory, but under careful manipulation the above method will give results of value for determining comparative activity of the guaiaconic acid oxidizing peroxidase in potato tubers.

The method described by GRÜSS (**2**) for obtaining a peroxidase solution from the potato tuber was first tried. According to this

method, morphologically similar parts of the tuber were sliced directly into absolute alcohol and heated to 70° C. for 10 minutes in order to destroy the oxidases. The slices were allowed to remain in alcohol 24 hours. The alcohol was changed three times. They were then dried between filter paper, covered with ether for a few minutes, replaced between filter paper, quickly dried in a vacuum desiccator, and thoroughly pulverized in a mortar. One gram of this powder was ground one minute with quartz sand and 25 cc. water and filtered. For the tests 5 cc. of the filtrate were used and 0.5 cc. of guaiaconic acid solution and 0.1 cc. of one-half per cent hydrogen peroxide. The guaiaconic acid solution was prepared by dissolving 0.5 gram of guaiaconic acid in 50 cc. alcohol.

Three sources of error were soon discovered in this method of extract preparation, which render it unreliable for comparative purposes. Filtering, which is necessary in order to obtain a sufficiently clear solution for colorimetric work, removes a large percentage of the peroxidase. This is probably due to inclusion of the peroxidase in the clot of coagulable proteins, and not to an insoluble form of the enzyme. Filtering has no effect on the peroxidase activity of fresh unheated extract.

TABLE I

EFFECT OF FILTERING ON PEROXIDASE ACTIVITY OF HEATED EXTRACT

HEATED TO 70° C. for 10 MIN.	SECONDS REQUIRED FOR REACTION TO REACH STANDARD TUBE		
	Unfiltered	Filtered through cotton	Filtered through paper
Sample 1	..	28	56
Sample 2	..	12	25
Sample 3	15	..	45
Sample 4	15	..	35

Another source of error probably arises also from the presence of coagulable proteins. The peroxidase leaches out of the coagulum and thereby renders the peroxidase activity of the solution very unstable, as shown in table II. HASSELBRING and ALSBERG (5) found a similar condition in studies upon oxidases. and first concluded that it must be due to coagulable proteins.

It is not due to activation of zymogen, as the phenomenon does not occur in the fresh unheated extract method described later.

TABLE II

SHOWS INCREASE IN PEROXIDASE ACTIVITY OF SOLUTION ON STANDING

	SECONDS REQUIRED FOR REACTION TO REACH STANDARD TUBE		
		After 2 hours	After 24 hours
Slices of potato dehydrated with alcohol and ether; heated to 70° C. for 10 min.	51	34	30

A third source of error, which would have to be taken into account, is the degree and time of drying. If the slices are dried in a desiccator for several hours, the peroxidase activity is greatly impaired. After a few days the peroxidase is practically destroyed in the powder produced by grinding the dried slices (table III). GORTNER (6) has recently described a tyrosinase, which loses its vitality on drying.

TABLE III

SHOWS LOSS OF PEROXIDASE IN POTATO WITH DRYING

Potato tuber	Time required for reaction to reach blue of standard tube
Slices dried in desiccator 30 min.	24 seconds
Slices dried in desiccator 22 hrs.	120 seconds
Powdered slices standing 4 days exposed to laboratory air	10 minutes

The above facts alone are sufficient to render the method described by GRÜSS of little value for determining peroxidase activity in conditions approaching those of the living tuber. By grinding the potato tuber with $CaCO_3$, thus neutralizing the acids, the peroxidase activity was found to be quite stable for some time in the resulting extract (table IV).

Based upon this fact the following procedure was employed for the final comparative determinations of the peroxidase in the potato tubers under investigation. The tubers were grated with frequent dipping of the surface in $CaCO_3$. The pulp was then

ground in a mortar with quartz sand for two minutes, and the extract pressed through cotton and cheesecloth; 1 cc. of the extract was at once added to 300 cc. of water. This dilution gave a solution sufficiently clear for the test and a speed of reaction which reached the standard color in less than a minute. It was unnecessary to destroy the oxidase by heating. In this dilute solution the time required for the oxidase to produce a visible blue was longer than that required for the peroxidase to produce the blue of the standard color.

TABLE IV

EFFECT ON PEROXIDASE ACTIVITY OF EXTRACT WHEN THE POTATO TUBER IS GRATED WITH $CaCO_3$

POTATO TUBER	SECONDS REQUIRED FOR REACTION TO REACH BLUE OF STANDARD TUBE		
		After 6 hours	After 24 hours
Ground with $CaCO_3$	21	21	30
Ground without $CaCO_3$.....	45	..	90

OXIDASE.—Colorimetric methods, as well as the direct measurement of the oxygen consumed by the oxidation of hydrochinon in the manner recommended by GRÜSS (**2**), were used in an effort to ascertain the comparative rate of oxidase activity. So many sources of error were discovered in applying these methods to the material under investigation, that the results were considered too unreliable for publication. Better methods than those in present use are much needed.

Experiments

In comparing results obtained by the two methods for peroxidase determinations previously described, it was found that the alcohol and ether method always gave a much greater peroxidase activity in the cold storage potatoes than in those stored at room temperature, while the fresh extract method gave practically the same in both cases during the same period of storage. According to the following table this would seem to be due to an alteration at low temperature of coagulate protein, which modifies the

amount of peroxidase occluded by clot, for after 24 hours of leaching the activity is just as great in the room-stored potatoes.

TABLE V

SHOWS INCREASE IN PEROXIDASE ACTIVITY IN COLD STORAGE POTATOES BY THE ALCOHOL AND ETHER METHOD, BUT NO INCREASE WHEN THE TESTS ARE MADE WITH FRESH UNHEATED EXTRACT

POTATO TUBER	SAMPLE	SECONDS REQUIRED FOR REACTION TO REACH STANDARD COLOR			
		Storage at 20°–25° C.		Storage at 0° C.	
			After 24 hours		After 24 hours
Slices treated with alcohol and ether; heated to 70° C. in alcohol for 10 minutes	1	60	20	25	20
	2	56		21	
	3	51		32	
Ground with $CaCO_2$ and determinations made with fresh unheated extract	1	35	42	35	40
	2	31		30	
	3	32		25	

The following table is a summary of the metabolic changes thus far studied occurring in a typical lot of young potatoes stored at 0° C. and 20–25° C. for a period of 6 weeks, tests being made every 2 weeks. Several lots were run, but as they all showed practically the same changes, only a typical table is given.

TABLE VI

SHOWS METABOLIC CHANGES OCCURRING IN POTATO TUBERS DURING AFTER-RIPENING AT LOW TEMPERATURE

EXPOSURE	TEMPERATURE	GLUCOSE	SUCROSE	STARCH	DIASTASE	CATALASE	PEROXIDASE
Days	° C.	Per cent	Per cent	Per cent	cc. potato extract to digest 100 cc. starch sol. in 24 hrs. at 48° C.	cc. of O_2 evolved in 3 min.	Seconds required to reach standard color
14	20–25	0.37	0.55	14.4	30	40.6	35
	0–+1	0.52	1.3	13.2	25	37.6	35
28	20–25	0.32	0.54	14.	30	41.2	33
	0–+1	1.8	1.65	11.	20	28.6	32
42	20–25	0.3	0.84	13.6	25	44.	32
	0–+1	3.5	1.8	9.6	20	26.4	25

Potatoes stored at 0° C. or below exude an acid fluid. This fact suggested the possibility that the increased diastatic activity after cold storage may be due to free acids. The decreased catalase activity might also be thus accounted for. The following single experiment is evidence in favor of this view.

Two potatoes of nearly equal weight were grated and thoroughly ground, one with $CaCO_3$, and the other without. Both were stored at 0° C. for 34 days, and analysis made according to table VII.

TABLE VII

EFFECT OF STORAGE AT 0° C. FOR 34 DAYS WHEN POTATO IS PREVIOUSLY GROUND WITH AND WITHOUT $CaCO_3$

POTATO GROUND	GLUCOSE	DIASTASE	PEROXIDASE	CATALASE
	Per cent	Units of extract to digest a unit of starch	Seconds required to reach standard color	cc. of O_2 evolved in 3 min.
Without $CaCO_3$	0.18	100	30	0.1
With $CaCO_3$	trace	160	40	6.7

The expressed potato sap is strongly acid. After repeated titrations, I found that the sap from cold storage potatoes and that from room-stored ones contained practically the same amount of acid. Low temperature, therefore, does not change the total acidity, but probably affects the permeability of protoplasmic membranes, and thereby allows the acids to reach zymogens more rapidly than under normal conditions.

Conclusion and summary

The method recommended by GRÜSS for determining the rate of peroxidase activity in the potato tuber gives no indication of the rate of activity in conditions approaching those of the living tuber. This is due to errors introduced by inclusion of the peroxidase in the clot of coagulable proteins, and to the loss of peroxidase during the process of drying the slices. After a few days the peroxidase is practically destroyed in the dry powdered potato. This method always showed an apparent increase in peroxidase activity in cold storage potatoes. The evidence at hand seems to indicate that this is due to an alteration of coagulable proteins

by low temperature, thus modifying the amount of peroxidase occluded by the clot.

Certain internal changes are accelerated by 0° C., which shorten the rest period of potato tubers.

Both glucose and sucrose accumulate. The increase in sucrose is more rapid at first than glucose, but by the end of 6 weeks of storage at low temperature the percentage of glucose is about twice that of sucrose.

Diastase activity was greater in the cold storage tubers than in those stored at room temperature at the end of 2 and 4 weeks; but at the end of 6 weeks there was no appreciable difference, as the variety used for this work was near the end of the rest period. A few had already germinated. The increased diastase activity is probably due to greater activation of zymogen by free acids, which are liberated by the greater permeability of protoplasmic membranes at low temperatures.

Catalase is very abundant in potato tubers stored either at 0° C. or at room temperature, but suffers a gradual reduction as storage at 0° C. continues. The presence of free acids would cause this reduction, as catalase is rapidly destroyed by the free acids in ground potato pulp. This behavior of catalase corresponds with that of respiration under similar conditions, a significant fact in the light of a recent claim (**3**) that catalase is the primary factor in alcoholic fermentation, and therefore probably in respiration.

A guaiaconic acid peroxidase is very active in potato tubers at the beginning of the rest period and increases slowly as the end of the rest period approaches. Low temperature had no appreciable effect in hastening this increase in the material used for this work, according to the method employed for its determination.

The changes peculiar to after-ripening may be in the buds, and the metabolism of the tuber as a whole may bear little or no causal relation to these processes.

The writer wishes to acknowledge his indebtedness to Dr. WILLIAM CROCKER for suggesting the problem and for his untiring interest and assistance during the progress of the work.

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CURRENT LITERATURE

NOTES FOR STUDENTS

Morphology of Nidularia.—In two papers FRIES has given a clear account of the morphology of the fruit-body and spore development of *Nidularia pisiformis* Tul. The first paper deals with the development of the fruit-body.[1] The youngest stages observed are nodules about 0.4 mm. in diameter. In the earliest stages these are differentiated into a uniform medulla and a cortex which become more pronounced later. All the cells are binucleate. The medulla soon becomes differentiated into a lower sterile portion and an upper denser portion in which the peridiola arise. The beginning of the peridiola is indicated by the appearance of islets of hyphae, rich in protoplasm, growing toward common centers. These hyphae represent the young hymenium. Later a cavity is formed by the expansion of these hyphae and those of the subhymenial layer. The peridiola, spherical at first, assume an oval form. A wall is formed around them, but this at first remains open at the poles. Through the openings the peridiola remain in connection with the surrounding medulla during their growth; the wall finally incloses the whole peridiolum. The development agrees in the main with the development of the fruit-bodies of other members of this peculiar group of Gasteromycetes, except that the peridiola are not connected to the wall of the fruit-body by strands of hyphae as in *Crucibulum* and *Cyathus*.

In the second paper[2] an account of spore development of the same plant is given. The young basidia are binucleate, agreeing in this respect with other Basidiomycetes, as well as with the ascus of Ascomycetes. The two nuclei grow to about twice the size of the vegetative nuclei, after which fusion takes place. This is followed by the usual rapid growth of the fusion nucleus just previous to the divisions leading to spore formation. The chromatin, which is in the so-called synapsis stage, later spreads out through the nuclear cavity in the form of an irregular band, which is single at first, but later appears to split lengthwise into two parallel threads. The chromatin thread shortens and thickens and breaks up into a number of double chromosomes. This process was not easily made out, but the author is inclined to believe that two such double chromosomes are formed, although some earlier stages seemed

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[1] FRIES, ROB. E., Om Utvecklingen af Fruktkroppen och Peridiolerna hos *Nidularia* (with German résumé). Svensk. Bot. Tidsk. **4**:126–138. *pl. 1. fig. 1.* 1910.

[2] ———, Ueber die cytologischen Verhältnisse bei der Sporenbildung von *Nidularia*. Zeitschr. Bot. **3**:145–165. *pls. 2.* 1911.

to show three to five segments. The spindle of the first division is transverse to the long axis of the basidium, as in the whole series of Basidiomycetes, beginning with the Tremellales. The processes of division are very obscure, but there appeared to be three or four chromosomes at each pole in the anaphase. The author interprets this as a heterotypic division, but believes that during the division the components of the double chromosomes become separated, thus accounting for the presence of four instead of two at each pole. The second division proceeds without reorganization of the daughter nuclei. It results in the distribution of the components of the double chromosomes to the new nuclei. Two chromosomes appear at each pole of the spindles. The whole interpretation hinges on the correctness of the author's assumption that only two segments are formed from the double chromatic band after synapsis.

After the reorganization following the second division of the nuclei, the sterigmata bud out from the basidia and swell out into spore bodies. Then the peculiar process of migration of the nuclei into the spore bodies takes place. The nuclei move to the upper part of the basidium and lose their membranes, leaving only the nucleolus and chromatin. The chromatin thread, with the nucleolus at its apex, then migrates through the narrow sterigmata into the spore cavity. This peculiar migration is explained by the fact that during the process the nuclei are in the prophase of a division which is completed as soon as the chromatin has entered the spore cavity. The mature spore is binucleate, corresponding in this respect with other Gasteromycetes that have been investigated.—H. HASSELBRING.

Hereditary factors in Primula.—The existence of numerous varieties of the Chinese primrose (*Primula sinensis*) makes this species an enticing one for the study of unit characters in inheritance, but the number of different factors is so great as to make complete analysis practically impossible. Factors for form of foliage, heterostylism, singleness of the flower, color of stems, color of flowers, palliators, inhibitors, pattern factors, coupling, and repulsion, are all needed in the description of the results. During the past eight years BATESON and GREGORY have been analyzing the characters which distinguish the different varieties, and they have jointly and severally reported on various phases of their results from time to time since 1903. GREGORY[3] has just presented a comprehensive memoir on these experiments, illustrated with three excellent double plates, two colored and one photographic. Some of the more interesting results may be mentioned. Long style is epistatic to short style; palmate type of leaf to the pinnate or "fern" type; crenate margins to entire margins; single flowers to double; the flower colors may be arranged in a series in such manner that each is epistatic to all that follow, as follows: dominant white, magenta, red, blue, recessive white; some pale

[3] GREGORY, R. P., Experiments with *Primula sinensis*. Jour. Genetics 1:73–132. *pls.* 3. 1911.

colors are recessive to the full colors, but more commonly the lighter shades are epistatic to the intense ones and are interpreted as the result of a partial inhibitor or "palliator"; there is similar epistasis of the lighter stem colors to the darker; two inhibiting factors produce definitely localized effects in the flower, one affecting the central region of the flower, the other the periphery. In all of these unit characters the expected Mendelian ratios were obviously present except in several instances of "repulsion" and of partial coupling. Thus magenta was never found associated with the short style, and a partial coupling between magenta flower color and green stigma seems to indicate that there is a segregation on the plan 7:1:1:7 in one of the sexes, while in the other sex the segregation follows the usual plan 1:1:1:1.

The occurrence of dominant and recessive white in the flower color of the different varieties presents an interesting situation. In the varieties first investigated, the dominant white was always associated with red stems and the recessive white with green stems. An exception to this rule exists in the case of the variety "Pearl," in which dominant white and green stems are combined. KEEBLE and PELLEW[4] now report an exception in the opposite direction in "Snow King," a red-stemmed variety with either dominant or recessive white flowers. Crosses between this variety and various colored varieties gave different results according as the particular individual of "Snow King" used in the cross chanced to be dominant, heterozygous, or recessive in regard to a dominant white factor *W*. The heterozygous whites when crossed with colored varieties gave white and colored, 1:1 in the F_1, and these F_1 whites when self-fertilized produced an F_2 which in each case closely approximated the expected ratio, 13 white: 3 colored.—GEORGE H. SHULL.

An inhibiting factor in oats.—NILSSON-EHLE[5] describes a number of instances in which mutants resembling the wild oats (*Avena fatua*) have appeared in his cultures of numerous cultivated varieties of *Avena sativa*, the coefficient of mutation being about 1 in 10,000. These atavists had approximately the same congeries of characteristics regardless of the characteristics of the varieties in which they were discovered. Most frequently they were found in heterozygous combination with the cultivated varieties, but sometimes also in the pure extracted forms. That these could not have been the results of crosses with the wild oats is proved by the fact that when they appeared in a variety having white or yellow glumes, the atavist retained this recessive character. The heterozygotes proved to be in all cases intermediate between the atavists and the particular varieties in which they appeared. The fact that the atavistic type differs in each case by a single unit character, so that the whole group of wild characters appears in their

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[4] KEEBLE, F., and PELLEW, MISS C., White-flowered varieties of *Primula sinensis*. Jour. Genetics 1:1–5. 1910.

[5] NILSSON-EHLE, H., Ueber Fälle spontanen Wegfallens eines Hemmungsfaktors beim Hafer. Zeit. Ind. Abstam. Vererb. 5:1–37. *pl.* 1. 1911.

usual combination in one-fourth of the F_2 offspring, leads the author to the conclusion that the difference between the wild oats and these various cultivated varieties is due to the presence in the latter of an inhibiting factor which prevents the development of the wild characters. As he has never found among the numerous crosses he has made between different cultivated varieties any instance in which the atavists made up one-sixteenth of the F_2, as they should do if different varieties possessed different inhibiting factors, he concludes that the same inhibiting factor is present in all the cultivated varieties, and that the different degrees of development of the awns and hairiness of the glumes which have been found to be dependent upon independent genes, must remain latent in the wild oats until the origin of an inhibiting factor brings them to light. On this ground he argues that the degree of discontinuity which results from any mutation depends upon the number of latent genes which are brought into manifestation by it, and also that various apparent correlations may result from the disappearance of a factor which had simultaneously inhibited both of the characters which appear to be correlated. The author does not take into account the hypothesis of "variable potency," which could also be made to explain how the same inhibiting factor in the various cultivated varieties could produce such various degrees of development of awns, hairiness of the glumes, etc., as are displayed by them.—GEORGE H. SHULL.

Mitosis in Spinacia.—This extensive investigation by STOMPS,[6] written in Dutch, but with an eleven page résumé in German, deals with mitosis in both vegetative cells and in the microspore and megaspore mother cells.

The $2x$ generation shows 12 chromosomes arranged in pairs, which can be distinguished not only in the nuclear plate but also in the prophase, and pairs probably persist in the resting nucleus. No continuous spirem is formed, the two components of each pair, as soon as they can be distinguished, having two free ends. A longitudinal splitting of the chromosome occurs in early prophase, a longitudinal row of vacuoles appearing, and these, by increasing in size, split the chromosome. This mode of splitting results in threads with alternating thickened and slender portions, but STOMPS does not regard the thickened portions as chromomeres or ids, nor does he regard the slender portions as linin, but both are the same in substance.

In the prophase of the reduction division, before synapsis, the 12 chromosomes fuse in pairs, forming 6, each with two free ends. There is not only a pairing, but also a genuine fusion of the two chromosomes of each pair. No continuous single or double thread is formed. As the nucleus comes out of synapsis, one sees 6 chromosomes, each evidently double, and the two mem-

[6] STOMPS, THEO. J., Kerndeeling en Synapsis bij *Spinacia oleracea*. 8vo. pp. 162. *pls.* 2. 1910. A briefer account in German, which is partly a summary and partly a translation of the original, is published in Biol. Centralbl. **31**: 257–320. *pls.* 1–3. 1911.

bers of a pair may separate at this stage. Tetrads sometimes occur at this time. The mantle fibers (*Zugfasern*) are believed to persist from one cell generation to another. The nuclear membrane is a tonoplast, and the nuclear cavity a complex of vacuoles.

Many of the figures look rather diagrammatic, but they are carefully drawn, and the summary indicates that the author, at least, feels certain of his principal conclusions. The work is so extensive and so well presented that it cannot be laid aside; cytologists should either confirm the conclusions or correct them.—CHARLES J. CHAMBERLAIN.

Fungi in rhizoids of liverworts.—Investigation of about thirty species of liverworts by GARJEANE[7] shows that there is no uniformity in the occurrence of fungi in the rhizoids. In some forms the presence of fungi seems to be the rule; in others, especially the bark-inhabiting forms, their presence seems to be the exception. In the same colony individuals with infected rhizoids often occur together with others not infected. The details of the mode of growth of the hyphae are described for *Lophozia inflata* and species of *Cephalozia* and *Cephaloziella*. From the details it appears that the plants in no way profit as a result of the presence of fungi in their rhizoids. On the contrary, the protoplasm in the young rhizoids, and also in the neighboring cells when these are infected, is killed by the fungi. Extended infection of rhizoids is accompanied by sickening of the plants. An interesting reaction of the rhizoids to the attack of the fungus is described in *Lophozia*. When the hypha comes into contact with a rhizoid, a thickening appears on the inside of the rhizoid wall opposite the point of contact. As the hypha grows into the cell, cellulose is continually deposited ahead of the growing point, so that the hypha is surrounded by a sheath of cellulose. Often hyphae pass straight through rhizoids in this way, and become incased in a tube of cellulose. The author was successful in isolating the same species of fungus, described as *Mucor rhizophilus*, from nine species of liverworts. A large number of successful infections was made with this fungus in sterile cultures of *Lophozia inflata*, *Cephalozia bicuspidata*, *Cephaloziella* sp., and *Jungermannia ventricosa*. The author believes that the association of fungus and rhizoid is not of the nature of a mycorhiza; neither does the fungus cause considerable damage to the plant, although strongly infected plants show the unfavorable influence of the fungus.—H. HASSELBRING.

Fall of petals.—FITTING[8] finds that a number of stimuli will cause the premature falling of the corollas of various sympetalous and polypetalous flowers. He worked in the main, however, with *Geranium pyrenaicum*. Among chemi-

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[7] GARJEANE, A. J. M., Die Verpilzung der Lebermoosrhizoiden. Flora **102**: 148–185. *pls. 11, 12. figs. 9.* 1911.

[8] FITTING, HANS, Untersuchungen über die vorzeitige Entblätterung von Blüten. Jahrb. Wiss. Bot. **49**:187–263. 1911.

cals that are effective are traces of illuminating gas and tobacco smoke; considerable concentrations of CO_2 (4–50 per cent); high partial pressures of ether and chloroform vapors; and HCl gas. Other effective stimuli are high temperatures, shaking, sprinkling with dust, and wounding the style. FITTING concludes that the process is a vital one, for it does not occur when the plant is in heat rigor or in rigor from lack of oxygen. He also concludes that it is a true stimulus process, showing well-marked presentation and reaction times, as well as typical summation and relaxation. The reaction cannot be attributed to general inhibitory and acceleration effects upon the flowering process, but is a direct stimulatory effect upon the petals. The reaction time varies greatly with the stimulus, age of flower, and species of flower. Traces of illuminating gas give a reaction only after 2–6 hours, while CO_2 in optimum concentration gave a reaction after 30 seconds in *Verbascum thapsiforme*, and after only a slightly longer period in a number of other forms. Reactions to shaking and high temperatures were also rapid. Old flowers were always more sensitive than young ones.

FITTING proposes to call these responses *chorisms*, using the prefixes chemo-, thermo-, seismo-, etc. The paper should prove of considerable economic interest.—WILLIAM CROCKER.

Fundamental units of vegetation.—Ecology as a definite branch of the science of botany, while still in its infancy, has reached a stage in its development at which it is instructive to take an occasional retrospective glance in order to inquire what were the beginnings from which the branch has developed and whether there are tendencies which require pruning or molding. Moss[9] has taken such a backward look over the course of the development of the concepts and the nomenclature of the units of vegetation most used in the study of plant communities. The look has been a careful one, and has traced "plant associations" from its first use in a floristic sense by HUMBOLDT, in 1806, and with its truer ecological meaning by SCHOUW, in 1822, to the present day. To Moss the concept seems to be best defined as "a community of definite floristic composition within a formation."

He finds "plant formation" a term and concept of slightly more recent origin, dating to its employment by GRISEBACH in 1838. The different meanings this term has had for various workers are discussed in such a manner as seems likely to lead to some agreement as to its proper content. The desirability of some general agreement as to methods of denoting associations and formations is discussed in a most reasonable manner, and several good suggestions made. The writer is to be commended for correctness of perspective and breadth of view throughout what is doubtless the best historical review of this phase of botany which has yet appeared.—GEO. D. FULLER.

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[9] Moss, C. E., The fundamental units of vegetation. New Phytol. **9**: 18–53. 1910.

Tropic responses.—In working out the phototropic responses of *Avena sativa*, ARISZ[10] believes he has shown that the terms reaction time, presentation time, threshold of stimulation, etc., do not represent any well-determined end points in tropic responses. Quotations from his paper present his conclusions: "Each quantity of energy reacts on the plant and is expressed by a curvature of definite maximum strength." "If we once more trace how far the above investigations influence our conception of the process of stimulation, it is clear that the similarity to physico-chemical processes becomes more and more marked. The existence of a threshold of stimulation can no longer be maintained, for not only is each quantity of energy perceived, but it is clear now that a reaction will always take place. The time which intervenes between the application of the stimulus and the beginning of the curvature, the 'reaction time,' was found to be experimentally undeterminable. Thus the latter cannot serve as a measure of sensitivenesss."

We are urged, then, in this stronghold of stimulus physiology (tropisms), to abandon the stimulus conception for the physico-chemical. BLACKMAN had earlier urged such a shift of viewpoint in the study of metabolic processes of plants.—WILLIAM CROCKER.

The cytology of rice.—Since closely related species or even races of a given species may show differences in chromosome characters, several races of rice (*Oryza sativa*) were selected by KUWADA[11] for a cytological study. Just before synapsis in the pollen mother cell, a number of chromatin masses, about equal to the diploid number of chromosomes, are found scattered throughout the nuclear cavity. The masses, which are constantly paired, stretch out into double threads, which remain double during synapsis, but fuse after the synaptic stage is past. Soon after synapsis, the single thread arising from the fusion again becomes double and segments into 12 bivalent chromosomes, or gemini, and throughout the prophases the two parts of the bivalent chromosomes remain in parallel association, while they become shorter and thicker. Even in the homotypic division paired chromosomes, forming pseudogemini, occur. In the diploid generation the chromosomes are always paired and the number is 24. The development of the embryo sac presents nothing unusual. There are at first three antipodals, but, as in other Gramineae, the number becomes much larger at a later stage in the development.—CHARLES J. CHAMBERLAIN.

Physics of transpiration.—RENNER[12] has already shown that in still air evaporation from surfaces of like shape but different size varies more nearly

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[10] ARISZ, W. H., On the connection between stimulus and effect in phototropic curvatures of seedlings of *Avena sativa*. Reprint from Proc. Konink. Akad. Wetensch. Amsterdam. March 25, 1911.

[11] KUWADA, YOSHINARI, A cytological study of *Oryza sativa* L. Bot. Mag. Tokyo **24**:267–281. *pl. 8.* 1910.

[12] Rev. in BOT. GAZ. **51**:156. 1911.

in proportion to the like linear dimensions of the surfaces than in proportion to the surfaces. He has also shown that for equal surfaces isodiametric surfaces give least evaporation, and that the greater the deviation from the isodiametric the greater the evaporation. These facts are related to the water vapor cap over the evaporating surfaces, a thing to which RENNER gives great importance in the absence of air currents. He concludes that the deviation from the linear dimension law, under conditions cited in the first sentence, is in large part due to convection currents set up by the moist air over the evaporating surface being less dense than the surrounding dry air. In the present work,[13] by means of wet filters and water surfaces, RENNER studied in great detail the effect of shape, size, position, and proximity of evaporating surfaces in both still and moving air. Later he expects to carry these studies over to leaves, where the part played by internal regulation can also be determined.—WILLIAM CROCKER.

Theories of heredity.—In a discussion of two theories of heredity, that the nucleus is and that it is not the sole bearer of hereditary qualities, LUNDEGÅRD[14] devotes most of his space to a study of the literature, but also describes the various constituents of the cell in root tips of *Vicia Faba*. In the first part of the paper he comes to the conclusion that the nucleus cannot be the sole bearer of hereditary characters, but that extra-nuclear structures must be considered. To the reviewer, the arguments do not seem conclusive. The second part deals with the structures variously known as mitochondria, chondriomitria, chondriosomes, etc., and with plastids and other bodies and substances found in cells. He believes that the mitochondria do not come from the nucleus, and that they are not bearers of hereditary qualities. Here again the reviewer is not convinced and, in the present state of the subject, is inclined to think that at least some of the bodies known as mitochondria are of nuclear origin. Plastids also are considered, and the view of SCHIMPER and others, that the plastid is a permanent organ of the cell, is upheld.—CHARLES J. CHAMBERLAIN.

Heterochromosomes.—That there is a differentiation among chromosomes has been recognized for some time by zoologists, but it is only more recently that botanists have turned their attention to the subject. In the wild mulberry (*Morus indica*) TAHARA[15] finds, in early stages of prophase in sporophyte nuclei, paired chromatin masses which may be called pronuclei, and even at

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[13] RENNER, O., Zur Physik der Transpiration. Ber. Deutsch. Bot. Gesells. **29**: 125–132. 1911.

[14] LUNDEGÅRD, HENRIK, Ein Beitrag zur Kritik zweier Vererbungshypothesen. Ueber Protoplasmastrukturen in den Wurzelmeristemzellen von *Vicia Faba*. Jahrb. Wiss. Bot. **48**: 285–378. *pls. 6–8*. 1910.

[15] TAHARA, MASATO, Ueber die Kernteilung bei *Morus*. Bot. Mag. Tokyo **24**: 281–289. *pl. 9*. 1910.

this early stage two pairs are noticeably larger than the rest, and the difference becomes more pronounced as the chromosomes become arranged in the equatorial plate. The usual number of chromosomes is 28, but it is often higher. In the mother cells there are constantly 14 bivalent chromosomes, or gemini, one pair constantly larger than the rest. While zoologists are assigning the large chromosome a particular function in the determination of sex, it is too early to make any statement for plants. At present what is needed is extensive investigation along the lines of the present paper.—CHARLES J. CHAMBERLAIN.

Crown gall and sarcoma.—In a recent review[16] of the bulletin on crown gall by SMITH, BROWN, and TOWNSEND, attention was called to the resemblance of the crown gall tumors to certain malignant animal tumors. SMITH has now issued a brief circular[17] to announce the discovery of further evidence of this resemblance. The bacterium causing the primary tumor occurs also in the secondary tumors, associated with the tumor cells, the conclusion being that this is not a disease which propagates itself independently of the inciting organism. Furthermore, "tumor strands" were observed connecting primary and secondary tumors, being deep-seated offshoots from the primary tumor which wedge their way through stems and leaves like foreign bodies and give rise to secondary tumors, which subsequently rupture through to the surface of the plant. The full details, with illustrations, are promised in another bulletin.—J. M. C.

Symposium on reproduction.[18]—At the meeting of the Botanical Society of America held at Boston, December 27–31, 1909, a symposium on the nuclear phenomena of sexual reproduction was one of the features. Dr. DAVIS discussed the nuclear phenomena of sexual reproduction in the algae, and Drs. HARPER, CHAMBERLAIN, and MOTTIER discussed the subject in the fungi, gymnosperms, and angiosperms respectively. No new investigations were presented, since the object was not to record the results of recent personal research, but rather to present the subject in such a way as to make it helpful to the botanical public, and to stimulate and facilitate research in the various phases of the problem. Naturally, the principal emphasis was laid on fertilization and reduction of chromosomes. No serious differences of opinion appeared, except in regard to alternation of generations.—CHARLES J. CHAMBERLAIN.

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[16] BOT. GAZ. **52**:75. 1911.

[17] SMITH, ERWIN F., Crown gall and sarcoma. U.S. Depart. Agric., Bur. Pl. Ind., Circular no. 85. pp. 4. June 20, 1911.

[18] DAVIS, B. M., HARPER, R. A., CHAMBERLAIN, CHARLES J., and MOTTIER, D. M., Nuclear phenomena of sexual reproduction in thallophytes and spermatophytes. Publication 45 of The Botanical Society of America. Reprinted from the American Naturalist of June, July, September, and October, 1910.

Germination of fern spores in darkness.—It has been almost the universal experience of those who have investigated the germination of fern spores that at usual room temperature and with so-called inorganic nutrition they will not germinate in complete absence of light. However, at high temperature, or in sugar or peptone solutions, germination in total darkness has been induced. FISCHER[19] has now found that the spores of one of the commonest and most widely distributed ferns, *Polypodium vulgare*, are able to germinate in darkness at 25° just as well as in light. This is probably the best case on record for germination in darkness, since prothallia were actually obtained, and not merely a bursting of the exospore, as LAAGE reported for *Osmunda regalis* and other ferns. The prothallia formed in darkness differ somewhat from those of the same age produced in light, being composed of more and longer cells. It is probable that some limiting factor prevents the germination of the spores of most ferns in darkness; and discovery of the proper conditions for germination may show that the spores of many species are capable of developing prothallia without light.—CHARLES A. SHULL.

Vegetation of Nockamixon Rocks and Navesink Highlands.—It is important to have on record the natural vegetation of areas that are becoming densely populated, since tracts that have escaped the modifying influence of the ax and the plow are being reduced to a minimum. HARSHBERGER has contributed much to this record, and has lately investigated[20] the plant formations on a series of cliffs, known as the Nockamixon Rocks, on the Delaware River in Pennsylvania. Upon the talus a climax mesophytic forest has developed, characterized by the beech, maple, and associated forms, with an oak forest upon the crest of the cliffs and a mixed one upon the larger rock shelves.

More recently he has studied the Navesink Highlands[21] upon the coastal plain of New Jersey. The forest is here dominated by the chestnut and the chestnut oak, with a more xerophytic association at the summit, characterized by dwarfed trees placed at wide intervals.—GEO. D. FULLER.

Plant remains in Scottish peat mosses.—LEWIS has published a fourth paper[22] upon this subject, the present investigation dealing with the Scottish Highlands and Shetland. An appendix also discusses the Icelandic peat deposits. His former conclusions as to the principal stages in the history of vegetation over peat-covered areas, since the later stages of the glacial period. were abundantly confirmed. The stages are as follows: (1) an arctic-alpine

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[19] FISCHER, HUGO, Licht- und Dunkelkeimung bei Farnsporen. Beihefte Bot. Centralbl. **27**[1]:60–62. 1911.

[20] HARSHBERGER, JOHN W., The plant formations of the Nockamixon Rocks, Pennsylvania. Bull. Torr. Bot. Club **36**:651–673. 1909.

[21] ———, The vegetation of the Navesink Highlands. Torreya **10**:1–10. 1910.

[22] LEWIS, FRANCIS J., The plant remains in the Scottish peat mosses. Part IV. Trans. Roy. Soc. Edinburgh **47**:793–833. *pls.* 5. 1911.

vegetation on the moraine deposited by the last ice sheet; (2) a forest of birch and hazel; (3) a layer of arctic-alpine plants, occurring down to sea level in Shetland; (4) a forest of pine, hazel, and birch, occurring up to 3200 feet; (5) a layer of peat, accumulated from stage 4 to the present day, consisting entirely of moorland plants. This means an alternation of two forest beds with two arctic beds, before the peat came in.—J. M. C.

The structure of Mesoxylon.—In 1910, SCOTT and MASLEN published *Mesoxylon* as a new genus of Cordaitales, which included five species. One of these, *M. Sutcliffii*, has now been studied by MASLEN,[23] so far as the structure of stem and leaf is concerned. The name of the genus refers to the fact of its intermediate position between *Cordaites* and *Poroxylon*, and the known species appear to bridge the gap almost completely. The present study confirms this original conclusion, the particular species studied being much nearer to *Cordaites* than *Poroxylon*. A condensed summary is given of the resemblances of *M. Sutcliffii* to each of these genera, and also its differences in each case. One of the most interesting features of *Mesoxylon* is that it illustrates the gradual extinction of centripetal wood and the establishment of endarch structures in the *Cordaites*.—J. M. C.

The chromosomes of Dahlia.—ISHIKAWA[24] finds 16 and 32 chromosomes in *Dahlia coronata*, but 32 and 64 in nine other species and races. In the pollen mother cells of *D. coronata* in the heterotypic prophase, the chromosomes are paired, but in the other species the pairing is seen also at the homotypic mitosis, indicating, according to ISHIKAWA, that the vegetative cells of these species are tetraploid.

From the literature and his own observations, the reviewer has tabulated the number of chromosomes in more than 30 species of composites, and finds that the number varies from 3–6 in *Crepis virens* to 21–42 in *Hieracium flagellare*, with 8–16 or 9–18 as the most usual numbers. The extraordinary variety of form in Compositae may be related to the variation in the chromatin.—CHARLES J. CHAMBERLAIN.

Proteolytic enzyme of Drosera.—The proteolytic enzyme of four species of *Drosera* (*D. auriculata*, *D. Menziesii*, *D. peltata*, *D. Whittakeri*) has been investigated by Miss JEAN WHITE,[25] who finds a pepsin-like enzyme present in all of them, but unassociated with any peptolytic or tryptic enzyme. Peptic digestion occurred either in acid, basic, or neutral medium, every test giving a good biuret reaction for peptones; but in no instance could the faintest trace of amides be found with the tryptophane reaction. This dis-

[23] MASLEN, ARTHUR J., The structure of *Mesoxylon Sutcliffii* (Scott). Ann. Botany **25**:381–414. *pls. 33–36*. 1911.

[24] ISHIKAWA, M., Cytologische Studien über Dahlien. Bot. Mag. Tokyo **25**:1–8. *pl. 1*. 1911.

[25] WHITE, JEAN, The proteolytic enzyme of *Drosera*. Proc. Roy. Soc. London B **83**:134–139. 1911.

covery is interesting, since it is the only record of a peptase occurring in plants unassociated with ereptase. The enzyme is present as such, not in the form of zymogen. The leaves of *Drosera* were found to be capable of absorbing dissolved peptones from liquids placed on their surfaces in a few hours.—CHARLES A. SHULL.

Hepaticae in Scotland.—MACVICAR[26] has published a full account of the liverworts of Scotland, stating that "this work may be regarded as a new departure for Scotland in this branch of botany," previous publications having been fragmentary. An ecological discussion of nearly 50 pages precedes the list, the latter including a full list of stations under each species. Among other interesting facts of distribution, the altitudes to which species ascend may be mentioned. Of the 225 species included in the list, 20 ascend above 4000 ft., 61 reach 3000–4000 ft., and 32 reach 2000–3000 ft.; which means that half of the Scottish species ascend above 2000 ft. There are 67 genera recognized in the list, those including 10 or more species being *Lophozia* (26), *Scappania* (20), *Marsupella* (13), and *Cephalozia* (10).—J. M. C.

A cretaceous Pityoxylon with ray tracheids.—It has been supposed that the occurrence of ray tracheids in the pinelike conifers is more recent than the Cretaceous, so that their discovery by BAILEY[27] in a *Pityoxylon* from the Upper Cretaceous of New Jersey is one of considerable interest. The species represents a structure intermediate between the older cretaceous pines and the most primitive of living pines; and the infrequent occurrence of ray tracheids in the older portions of the stems and their entire absence from the younger wood are taken to indicate that these structures are of recent origin and are not strongly fixed upon the plant. This shifts the development of ray tracheids from the Tertiary to the Upper Cretaceous.—J. M. C.

Longevity of seeds.—Miss REES[28] has made a study of the relation existing between the structure and permeability of the coats and the longevity of seeds. In general, the macrobiotic seeds (retaining vitality for more than 15 years) belong to the legumes and have highly cutinized coats. *Eucalyptus calophylla* and *E. diversicolor* are exceptions. They possess no impervious covering, and, contrary to the general situation for macrobiotic seeds, they are large and very rich in oils.—WILLIAM CROCKER.

Laboratory air.—NELJUBOW[29] has studied the growth of the pea seedling in laboratory air and comes to the following conclusions: Ethylene is the

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[26] MACVICAR, SYMERS M., The distribution of Hepaticae in Scotland. Trans. and Proc. Bot. Soc. Edinburgh **25**:vi+336. 1910.

[27] BAILEY, I. W., A cretaceous *Pityoxylon* with marginal tracheids. Ann. Botany **25**:315–325. *pl. 26*. 1911.

[28] REES, BERTHA, Longevity of seeds and structure and nature of the seed coat. Proc. Roy. Soc. Victoria N.S. **23**:393–414. 1911.

[29] NELJUBOW, D., Geotropism in der Laboratoriumsluft. Ber. Deutsch. Bot. Gesells. **29**:97–112. 1911.

effective impurity of the laboratory air. Acetylene in sufficient concentration has the same effect. In these impurities the seedling loses its negative geotropism and becomes transversely geotropic or diageotropic. All his conclusions, with much more data for substantiation than NELJUBOW has, were reported by KNIGHT and his co-workers at the Boston meeting of the A.A.A.S. in 1910. Extracts of this report appear in *Science*[30] and in the *Experiment Station Record*.[31]—WILLIAM CROCKER.

Height of the Douglas fir.—Inquiring into the cause of the great height of the Douglas fir, FRYE[32] finds that unusual size is a characteristic of many of its neighbors, and cites as an example the common brake, which in this region attains a height of 14 feet. This among other things leads to the supposition that the cause of such giants of vegetation is to be sought in the climate, and hence to the conclusion that the fir is tall because it grows in a damp climate and in conditions of partial darkness due to overcrowding and to the large number of dark days during its elongating season.—GEO. D. FULLER.

The chromosomes of Ginkgo.—Conflicting accounts by CARDIFF, CAROTHERS, and SPRECHER regarding the number of chromosomes in *Ginkgo biloba* led ISHIKAWA[33] to examine the readily accessible Japanese material. He found 12 bivalent chromosomes in the pollen mother cell, the number reported by CARDIFF. One of the 12 is constantly larger than the other 11, a fact recorded in the figure but not in the text of both CARDIFF and CAROTHERS. While the paper is short, the evidence that 12 is the gametophytic number of chromosomes in *Ginkgo* is conclusive.—CHARLES J. CHAMBERLAIN.

The embryo sac of Pandanus.—From material of *Pandanus coronatus* collected in Java, CAMPBELL[34] finds that the embryo sac has a nearly normal egg apparatus, an endosperm nucleus formed by the fusion of two or more nuclei, and a considerable mass of antipodals, resembling the antipodal situation in *Sparganium*, except that in *Sparganium* most of the antipodals are formed after fertilization. CAMPBELL had already noted as many as 14 nuclei in the embryo sac of *Pandanus* before fertilization.—CHARLES J. CHAMBERLAIN.

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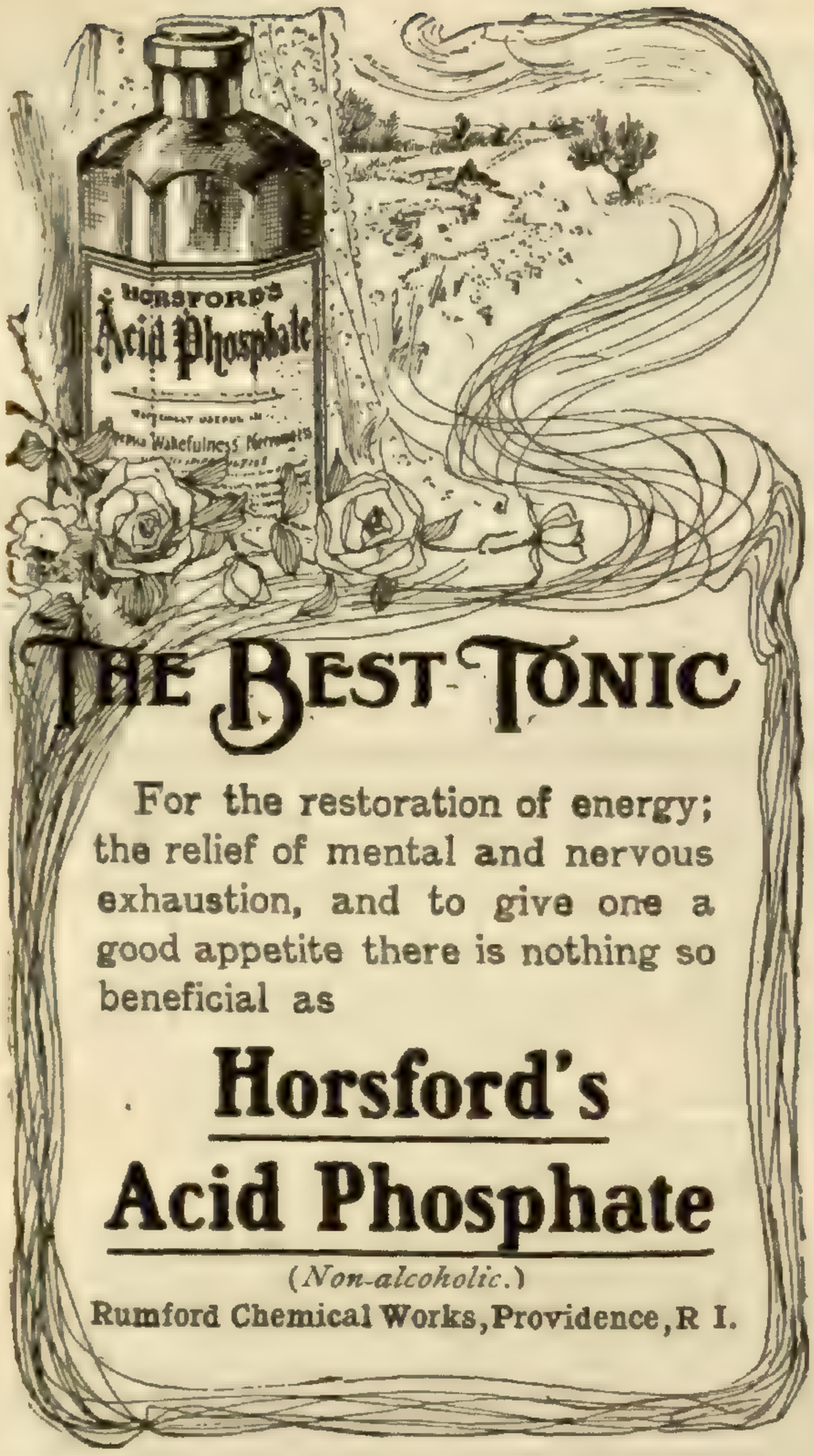
[30] KNIGHT, LEE I., ROSE, R. CATLIN, and CROCKER, WILLIAM, Effect of various gases and vapors upon etiolated seedlings of the sweet pea; a new method of detecting traces of illuminating gas. Science N.S. **31**:635, 636. 1910.

[31] Exp. Sta. Rec. **23**: 229, 230. 1910.

[32] FRYE, T. C., Height and dominance of the Douglas fir. Forestry Quart. **8**: 468–470. 1910.

[33] ISHIKAWA, M., Ueber die Zahl der Chromosomen von *Ginkgo biloba* L. Bot. Mag. Tokyo **24**:225, 226. *figs.* 3. 1910.

[34] CAMPBELL, D. H., The embryo sac of *Pandanus coronatus*. Bull. Torr. Bot. Club **38**:293–295. 1910.



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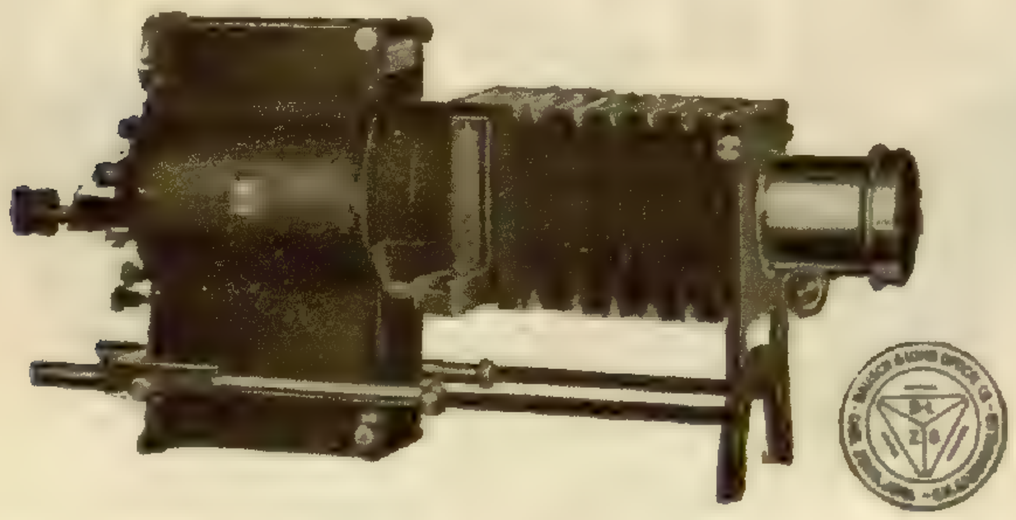

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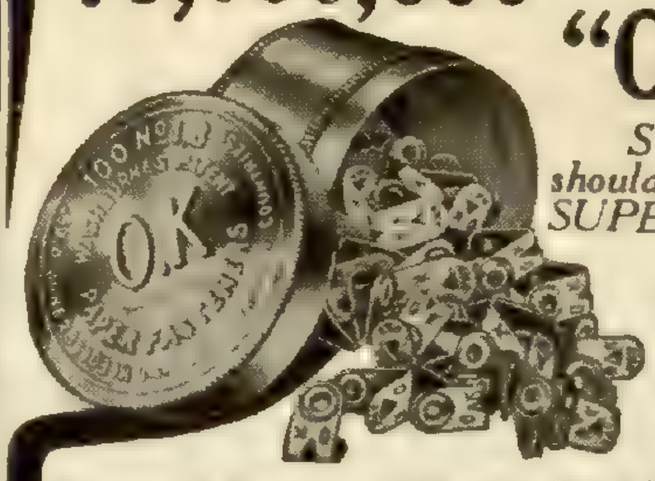

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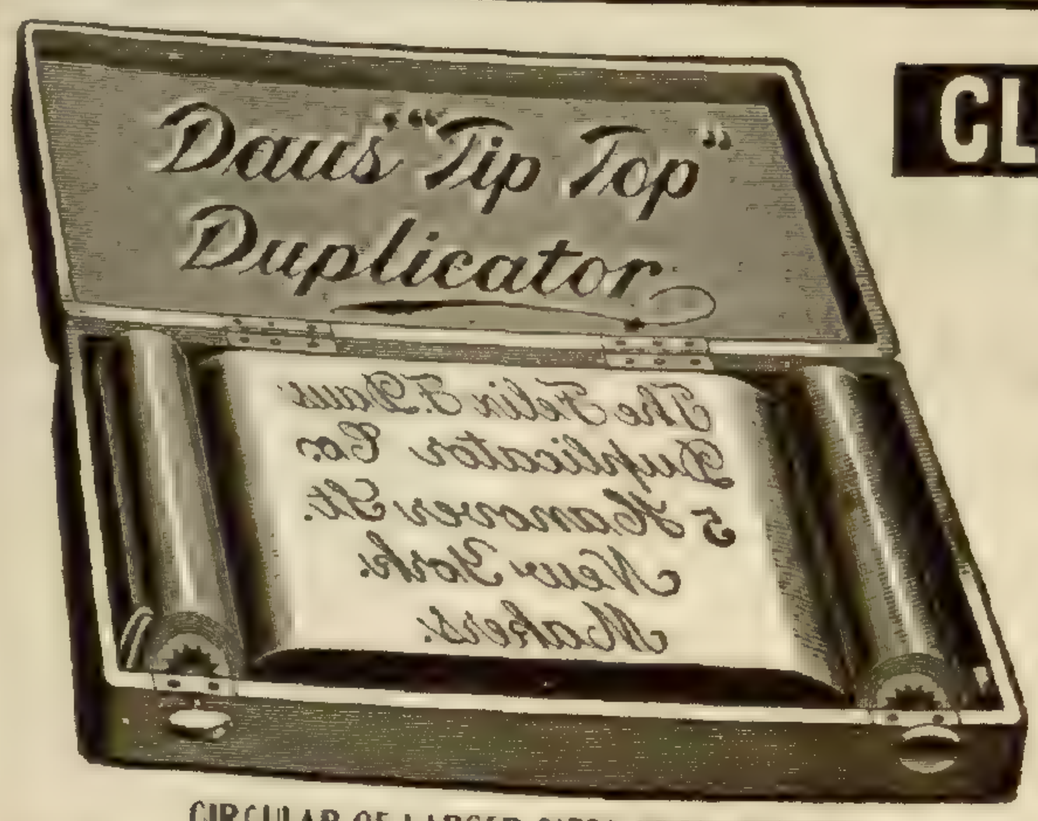

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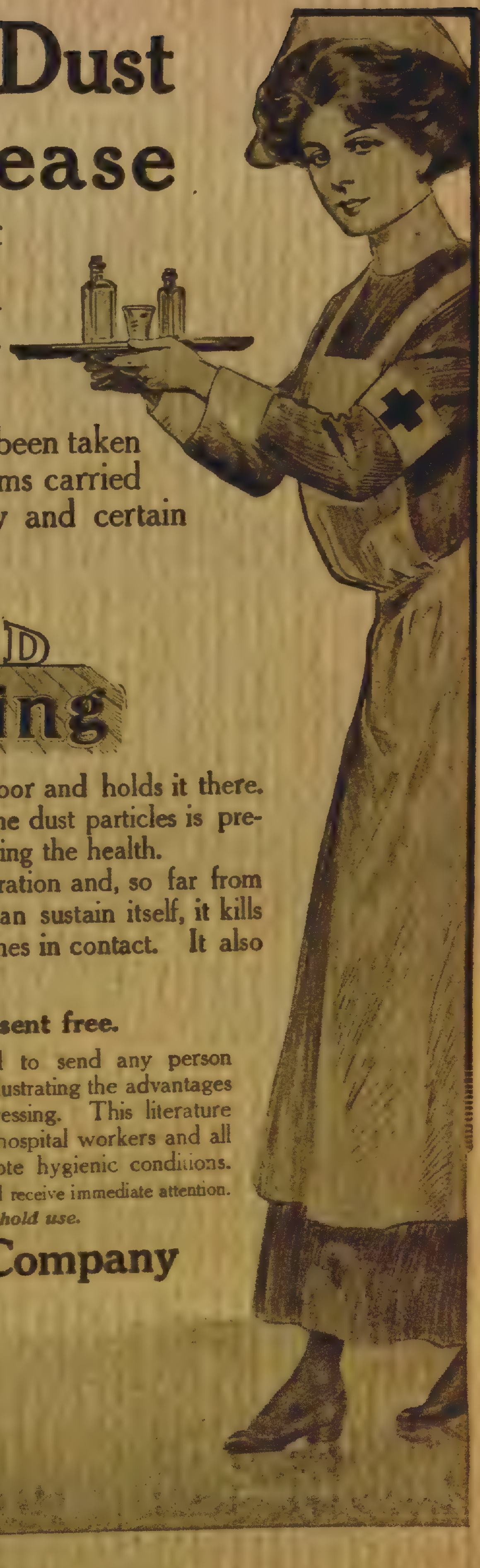

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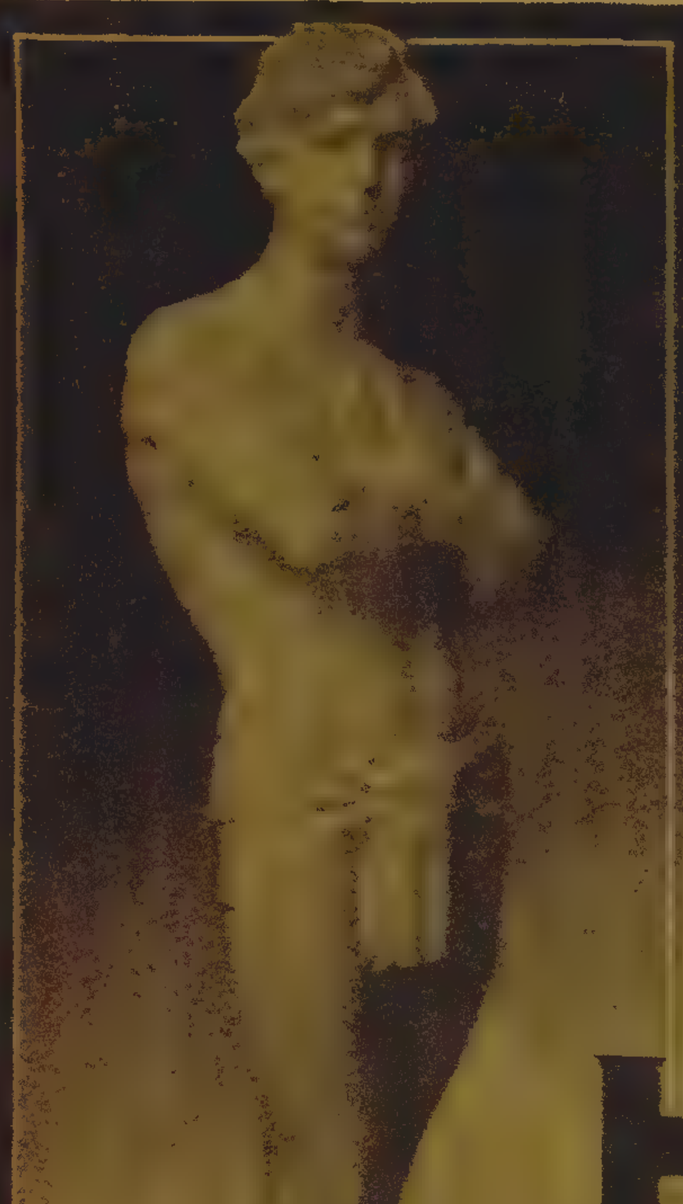

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THE

BOTANICAL GAZETTE

NOVEMBER 1911

REVERSIBLE SEX-MUTANTS IN LYCHNIS DIOICA[1]

GEORGE HARRISON SHULL

(WITH FIFTEEN FIGURES)

Six hermaphrodite specimens of *Lychnis dioica* L. were found in cultures of 1908, and eight in 1909. With respect to their hereditary behavior in the first generation, when used as pollen parents, these hermaphrodites proved to be of two kinds, the individuals *A* and *B* being capable of determining the hermaphrodite character in their male offspring, while individuals *C* and *D* behaved exactly like normal males, giving progenies consisting of females and normal males.

The conclusion was reached (SHULL **26**) that the hermaphrodites are modified males, because (1) in all families in which the first mentioned type of hermaphrodite was used as the pollen parent the offspring consisted of females and hermaphrodites in the same ratio as would have been expected of females and males if a normal male had been used as the pollen parent, and because (2) the second type of hermaphrodite when used as a pollen parent gave the same result that a normal male would have given.

Accepting tentatively the Mendelian explanation of sex first clearly enunciated by CORRENS (**6**), which recognizes the one sex as homozygous and the other sex as heterozygous with respect to a sex-producing gene, it was decided that these hermaphrodites (and therefore also males) must be heterozygous, because (1) the males are capable of being modified in such manner as to display function-

[1] Read at the meeting of the Botanical Society of America, Minneapolis, December, 1910.

al organs of both sexes, and because (2) self-fertilized hermaphrodites produce dimorphic progenies, consisting of females and hermaphrodites.

In my first paper on the inheritance of sex in *Lychnis* (SHULL **26**), I represented the sex genes by the conventional signs for the sexes (♀, ♂, and ☿). As these signs were used in my tables with two different meanings—to represent sometimes the character of the genes and at other times the character of the soma—I suspect that readers may have experienced some difficulty in comprehending the tables. I shall therefore adopt here the plan usually followed by students of genetics, of representing the genes by letters, letting *Ff* be respectively the presence and absence of a female determiner, *Mm* a male determiner, and *Hh* a hermaphrodite determiner. The conventional signs for the sexes will be used in this paper only in their more usual signification, referring to the nature of the soma, that is, the sporophyte.

If CORRENS' view of sex determination is correct, and the males are heterozygous, the females must be homozygous. CASTLE (**5**) suggests that in such a case the females will always be *positive* homozygotes, having a pair of sex genes (*FF*) corresponding with a single equivalent gene (*Ff*) in the male. I do not believe that this view can be substantiated, as there seems no good reason why females should not be negative homozygotes in some plants and animals, "neutral" homozygotes in others, and positive homozygotes in a third class. If the females are positive homozygotes, the somatic formula of the two sexes may be represented thus: *FF*=♀, and *Ff*=♂; if the females are negative homozygotes, the corresponding symbols will be *FFmm*=♀, and *FFMm*=♂; and if the female is a "neutral" homozygote, the formulae of the two sexes will be *FF*=♀, and *FM*=♂. Only the first two of these assumptions concerning the nature of the females were considered in my earlier paper, and either was found capable of explaining the results secured in the first generation, provided the presence of a partially independent hermaphrodite factor (*H*) might also be assumed.

Whether there was any genetic relationship between the hermaphrodites *A* and *B* which produced hermaphrodite offspring, and *C* and *D* which produced males, could not be determined in the first

generation, and two explanations seemed possible: (1) these two types of hermaphrodites might be respectively homozygous and heterozygous in regard to a modifying factor *H*, whose presence was assumed, on the suggestion of CORRENS, as possibly necessary for the change of a normal male into a hermaphrodite; (2) the hermaphrodites of the second type (*C* and *D*), which gave first generation progenies equivalent to those produced by normal males, might owe their hermaphrodite character to some accident of development which affected the soma alone, leaving the germ cells unchanged. In this case they might be appropriately called "somatic hermaphrodites," to distinguish them from those of the first type (*A* and *B*) which transmitted the hermaphrodite character to their male offspring and which are therefore to be recognized as "genetic hermaphrodites" or true hermaphrodite mutants.

Neither the character of the females nor the relationship of the two types of hermaphrodites could be determined from the results of the first generation, but it was obvious that at least a partial solution could be expected from the second generation. To attain this end a large number of crosses were made in 1909, by using hermaphrodite individuals and their derivatives in various combinations with each other, with unrelated females, and with normal males. The offspring of these crosses were grown during the summer of 1910, and the 104 families produced from them included 6132 individuals which came to bloom and of which the sex was recorded. These records were made in the writer's absence by Mr. R. CATLIN ROSE, to whose energy, faithfulness, and care it gives me pleasure to testify.

In order to comprehend fully the problems involved, it will be advantageous to consider some assumptions which were permitted by the results of the F_1 crosses, and whose availability is partially tested in the F_2 families reported in the present paper. In this connection it is also important to consider briefly the "presence and absence" hypothesis, a full discussion of which, however, would require too great a digression. Although this so-called hypothesis is frequently referred to by students of genetics, I am not aware that it has ever had a very definite formulation, and it would undoubtedly be defined differently by different students.

"Presence and absence" came into use in the first place, simply as a convenient method of expression to avoid the confusion which arises when the same dominant character is described as an alternative of several different characters which are hypostatic to it, and which may themselves be present or absent in any particular instance. The very general applicability of this mode of expression naturally suggested to various writers (HURST 18, SHULL 27, etc.) that it might have a more fundamental significance than merely as a convenient form of description. These authors considered it simpler and more practical to suppose that the heterozygous genes are unpaired, and that the "*absence*" of a character[2] is unrepresented by any internal unit corresponding with the gene which determines the "*presence*" of that character. The "presence and absence" hypothesis need not be associated, however, with the conception of unpaired determiners in the heterozygote, for in any *pair* of organs there may be present a function or feature in one member of the pair which is absent in the other member, or both members may be alike in kind but different in quantity or activity, the differential between the two being in this case the determiner of the alternative characters involved. This excess in one member of the pair would be present, of course, in that member only, and must be absent in its mate. Whether the hypothesis of unpaired genes or that of paired genes represents the true condition in any particular instance, and whether the absence of a character is absolute or only relative, will not interfere in the least with the use of "presence and absence" as the most convenient method of stating a great majority of the alternative characters with which the student of heredity has to deal. For the application of these different phases of the "presence and absence" hypothesis to the sex problem in *Lychnis*, attention is directed to the following table:

[2] It is to be regretted that some writers have misconstrued the meaning attached by most geneticists to the expression "absence of a character." The absence of the Angora character in cats, rabbits, etc., does not result in a hairless animal, but one with short hair. In *Oenothera* the absence of *rubricalyx* pigmentation does not prevent the production of anthocyan in the amount and localization characteristic of *O. rubrinervis* (see GATES, R. R., Studies on the variability and heritability of pigmentation in *Oenothera*. Zeitsch. Ind. Abst. Vererb. 4:337–372. 1911).

TABLE I

PRIMARY ASSUMPTION I.—There is a separate factor *H* which changes the male to a hermaphrodite, but which cannot find expression in the female.

SECONDARY ASSUMPTION I.—The two types of hermaphrodite are respectively homozygous and heterozygous in the factor *H*.

WHEN THE FEMALE IS	FORMULAE		REQUIRED ASSUMPTION	HYPOTHETICAL COMBINATIONS	EMPIRICAL RESULTS	REMARKS
	female	hermaphrodite				
Positive, and						
H homozygous	*FFhh*	*FfHH*	.....	*FFHh* and *FfHh*	♀ and ☿	
H heterozygous	*FFhh*	*FfHh*	*H* coupled with *F* in heterozygote	*FFHh* and *Ffhh*	♀ and ♂	
Negative, and						The correctness of these assumptions would result in: F_1 ♀'s with latent *H* F_1 ☿'s unlike P_1 ☿'s.
H homozygous	*FFmmhh*	*FFMmHH*	.....	*FFmmHh* and *FFMmHh*	♀ and ☿	
H heterozygous	*FFmmhh*	*FFMmHh*	*H* allelomorphic to *M* in heterozygote	*FFmmHh* and *FFMmhh*	♀ and ☤	
Neutral, and						
H homozygous	*FFhh*	*FMHH*	.....	*FFHh* and *FMHh*	♀ and ☿	
H heterozygous	*FFhh*	*FMHh*	*H* coupled with *F* in heterozygote	*FFHh* and *FMhh*	♀ and ♂	

TABLE I—*Continued*

SECONDARY ASSUMPTION II.—The second type of hermaphrodite is purely somatic and unrelated to the first type, and the first type is then heterozygous in respect to *H*.*

WHEN THE FEMALE IS	FORMULAE		REQUIRED ASSUMPTION	HYPOTHETICAL COMBINATIONS	EMPIRICAL RESULTS	REMARKS
	female	hermaphrodite				
Positive, and						
Genes unpaired	*FFhh*	*FfHh*	*H* allelomorphic to *F*	*FFhh* and *FfHh*	♀ and ☿	♀'s cannot transmit hermaphroditism
Genes paired ..	*FFhh*	*FfHh*	*H* coupled with *f*			
Negative.....	*FFmmhh*	*FFMmHh*	*H* coupled with *M*	*FFmmhh* and *FFMmHh*	♀ and ☿	F_1☿'s are like P_1☿'s
Neutral.....	*FFhh*	*FMHh*	*H* coupled with *M*	*FFhh* and *FMHh*	♀ and ☿	

PRIMARY ASSUMPTION II.—There is no factor *H*, hermaphroditism being caused by a mutative modification of the sex gene, which may then be represented by M_H, F_H, or f_H.

Positive, and						
Genes unpaired	*FF*	F_Hf	.....	None that could result in	♀ and ☿	The ♀ cannot be positive unless *F* has a synaptic mate
Genes paired ..	*FF*	Ff_H	Chance distribution	*FF* and Ff_H	♀ and ☿	
Negative.....	*FFmm*	FFM_Hm		*FFmm* and $FFMm_H$	♀ and ☿	♀'s cannot transmit hermaphroditism
Neutral.....	*FF*	FM_H		*FF* and FM_H	♀ and ☿	F_1 ☿'s same as P_1 ☿'s

* The case in which *H* is homozygous in the genetic hermaphrodites has been already tabulated under secondary assumption I.

Particular attention should be given to only two points in this table until after the results secured in the second generation have been considered. The assumptions which form the basis of the first section of the table lead to the expectation (*a*) that females derived from hermaphrodite families, whether they be fertilized by normal males or by their hermaphrodite sibs, will yield families in which the male offspring are hermaphrodite and normal male in equal numbers; and (*b*) that the hermaphrodites of the second generation when used to fertilize females from normal male families will produce no hermaphrodites, but only females and males. The alternative assumptions involved in the second and third sections of the table, on the other hand, lead to the expectation that, regardless of the origin of the female, no hermaphrodites will be produced normally, except when fertilization is brought about by sperms from a genetic hermaphrodite, and then the result will always be the same whether this hermaphrodite was a mutant or whether it was derived from an antecedent hermaphrodite.

We may now proceed to examine the results of the crosses. This will be most easily accomplished by considering each type of cross separately in the following fourteen cases. In the model pedigrees, illustrated under each case, the oldest ancestors entered in the diagrams are females and males both of which came from normal families, whose matings had been controlled during at least three still earlier generations, and which are known to have been in each such previous generation the result of crosses between females and normal males, and to have belonged to families in which no hermaphrodite mutants appeared. In the diagrams all male and hermaphrodite individuals which appeared as mutants are indicated as such, and it should be understood that any male or hermaphrodite not so marked was a member of a family which consisted of a normal proportion of its own type, that is, either male or hermaphrodite.

CASE I

Crosses of genetic hermaphrodite mutants with females

Only 2 of the 8 plants recorded as hermaphrodites in 1909, in otherwise normal male families, were successfully used for breeding. One of these, bred to 2 different unrelated females, produced 72

females and 88 hermaphrodites (nos. 09123 and 09171). The other, bred to the same 2 females, produced 116 females and 53 hermaphrodites (nos. 09124 and 09172). The result of these four crosses, involving 2 hermaphrodite mutants, was therefore 188 females and 141 hermaphrodites, thus showing that these 2 hermaphrodite mutants were of the same character as the two denomi-

Pedigree no.	Result	Pedigree no.	Result
0869	58♀:36☿:1♂	08150	59♀:43☿
08106	53♀:50☿	09123	36♀:53☿
08118	60♀:40☿:1♂	09124	52♀:30☿
08127	51♀:52☿	09171	36♀:35☿
08128	50♀:51☿	09172	64♀:23☿
08149	67♀:33☿	Total	586♀:446☿:2♂

nated *A* and *B* in my earlier report. For the sake of completeness, the crosses of *A* and *B* already reported are included in the tabulation of these crosses, the total progeny from this type of cross being 586 females, 446 hermaphrodites, and 2 males.

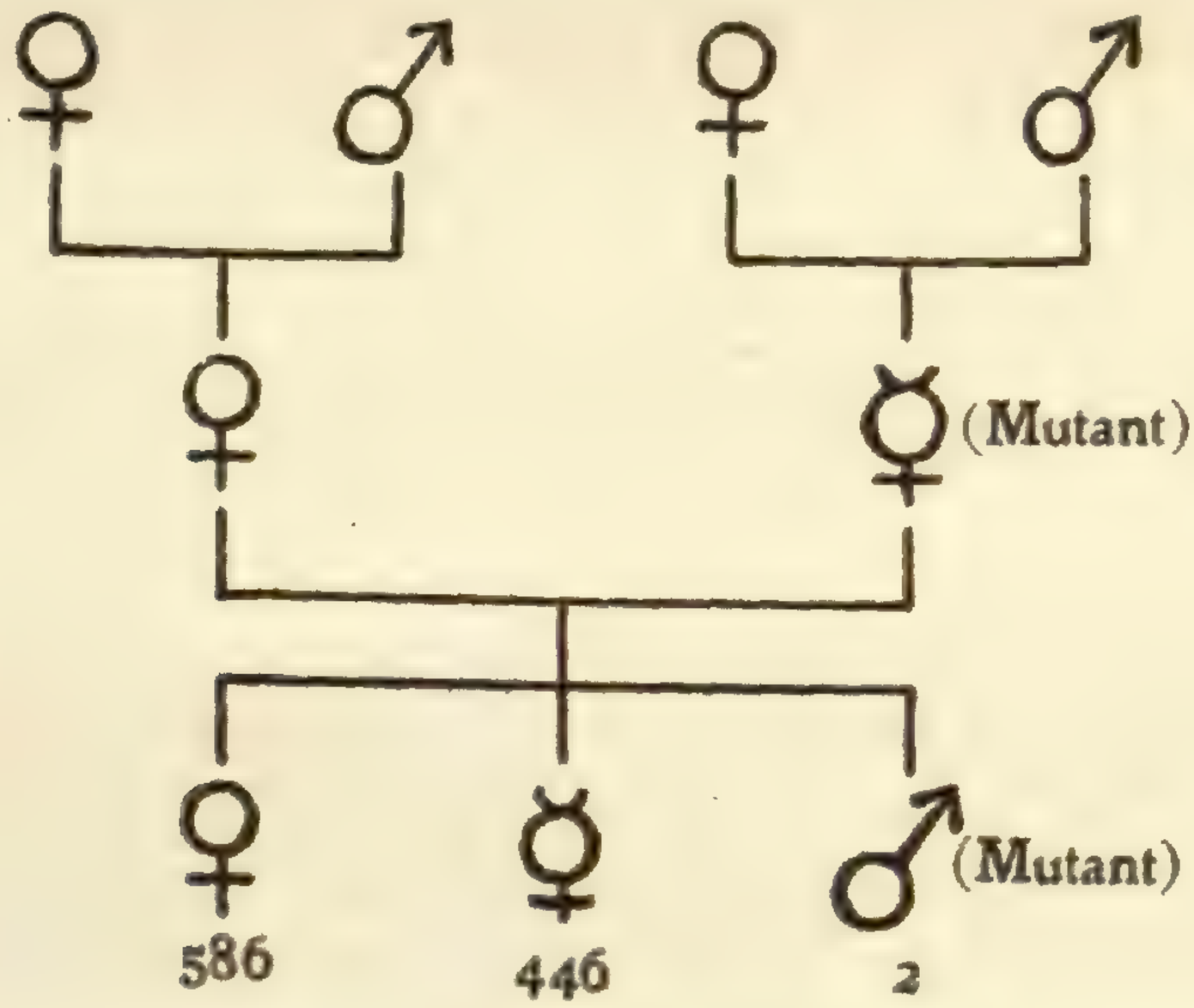

FIG. 1.—Model pedigree for case I

Two other individuals, which had a derangement of the sexual characters of such a nature that the lobes of the calyx were transformed into stigmas, and in one instance a small ovary with apparently functional stigmas was present in the center of the flower and

associated with functional stamens, were of such anomalous character that they have not been included among the 8 recognized hermaphrodites found in normal families in 1909, but they will be mentioned later under case XIII in connection with the somatic hermaphrodites *C* and *D* of my preliminary report.

CASE II

When genetic hermaphrodite mutants are self-fertilized

Pedigree no.	Result
08115	24♀: 19☿
08117	9♀: 6☿
08119	110♀: 95☿
Total	143♀:120☿

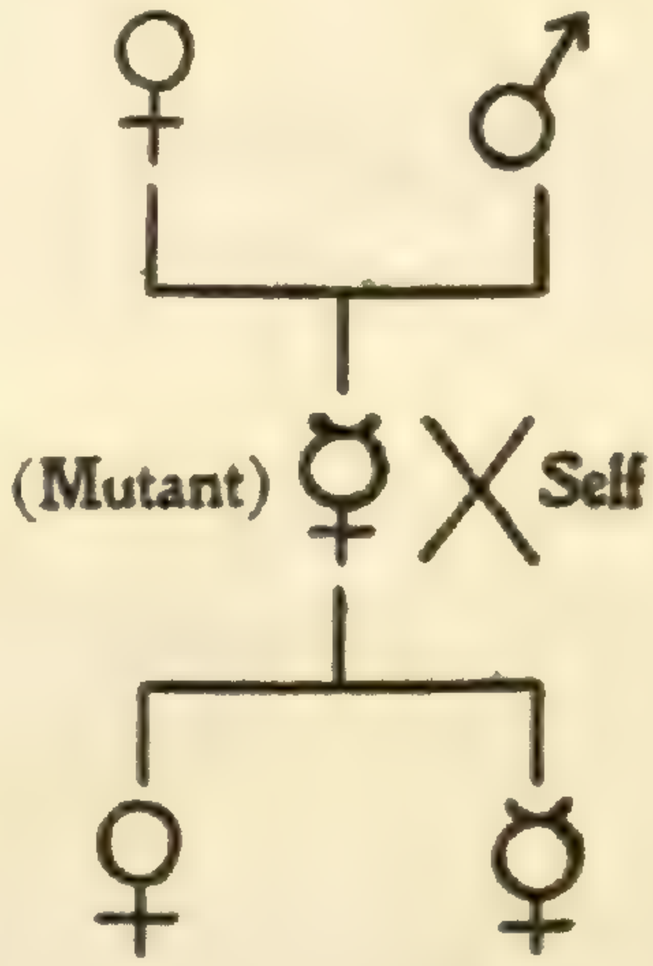

Fig. 2.—Model pedigree for case II.

None of the new hermaphrodite mutants discovered in 1909 were successfully self-fertilized, and the pedigrees here reported are repeated from my former paper for the sake of completeness. All the self-fertilized hermaphrodites which yielded progenies in my 1910 cultures belonged to a later generation, being offspring of a self-fertilized hermaphrodite and not the progeny of new mutants. They consequently belong to a separate case and will be considered next. The agreement of these results with those under case I leads to the conclusion that the eggs of the hermaphrodite are all of one type, that is, female-bearing, like those of the females. The significance of this result will be considered later.

CASE III

When F_1 hermaphrodites are self-fertilized

Pedigree no.	Result
09185	5♀: 8☿
09186	17☿: 6♀
09187	18♀:23☿
09191	6♀:10♀:1♂
09216	1♀
09217	16♀: 9☿
09218	17♀: 1♂
09219	22♀: 5☿
09220	2♀: 2☿
09222	43♀:38☿:1♂
Total	147♀:101♀:3♂

The first four of these families were produced by self-fertilizing 4 individuals of pedigree number 08115, and the rest by self-fertilizing 6 individuals of number 08119. Most of these families were too small to show obvious differences in the genetic composition of the different parent plants, or between them and the hermaphrodite mutants tested under case II. The small size of the families is due to the comparatively poor development of the ovaries and stigmas in most hermaphrodites, and the consequent difficulty of securing large quantities of seeds by self-fertilization. Most of the attempts to self-fertilize the hermaphrodites resulted in failure, and only in a small proportion were any seeds produced. The total result agrees with results secured from the observation of larger families, and it is fair to assume that the relatively large differences shown by some of these families are not significant because of the smallness of the progenies. This conclusion will be fully justified I believe, when it is observed under case IV that the very same plants, which produced the somewhat variable progenies shown above, gave uniform results when they were crossed with an unrelated female.

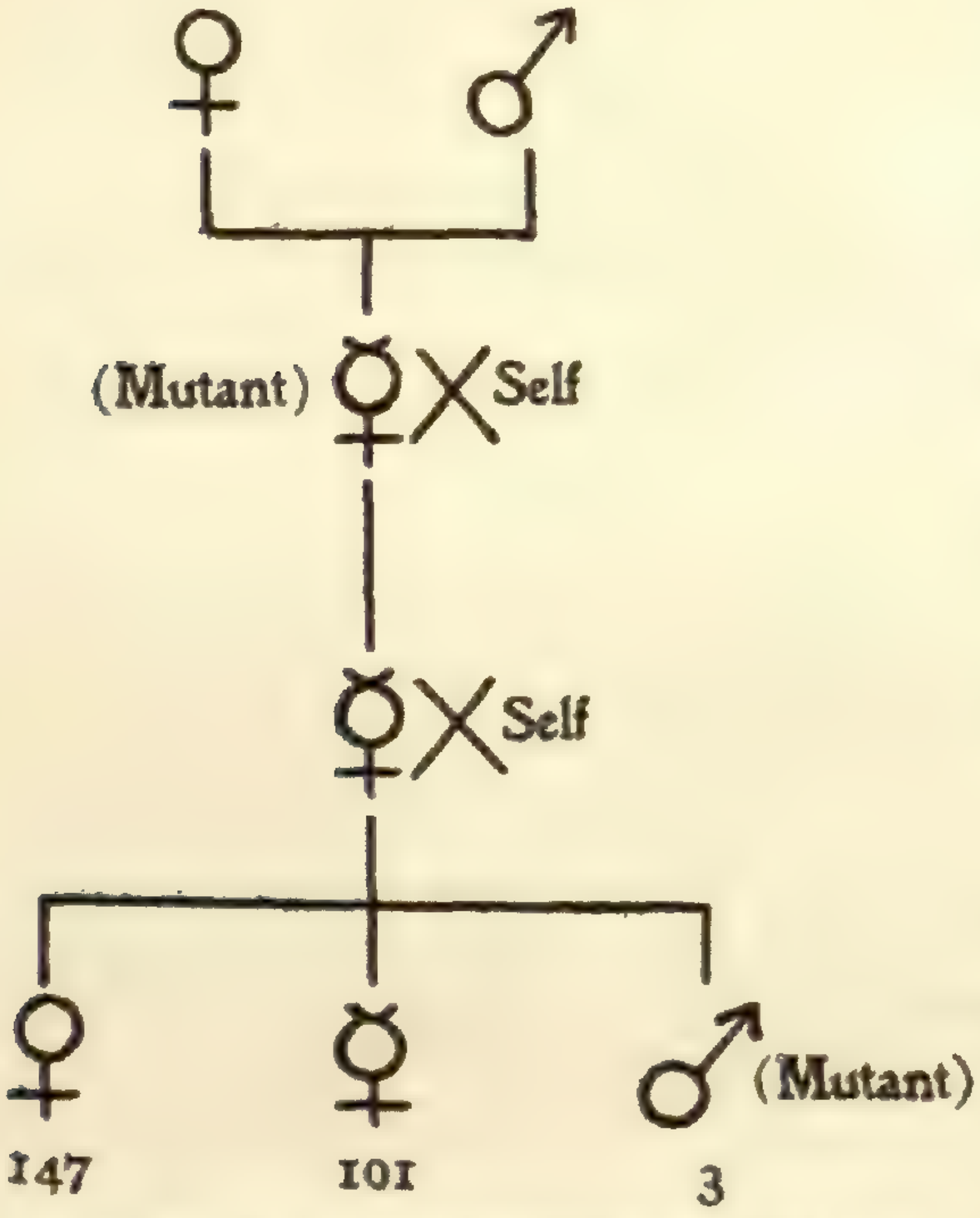

FIG. 3.—Model pedigree for case III

CASE IV

WHEN HERMAPHRODITES FROM THE PROGENY OF A SELF-FERTILIZED HERMAPHRODITE MUTANT ARE CROSSED WITH AN UNRELATED FEMALE

The families 09133 to 09142, inclusive, resulted from pollinating different flowers of a single female, 08114(4), with the pollen from 10 different hermaphrodites taken consecutively in family 08115, and the remaining 19 families were produced by pollinating the same female, 08114(4), with pollen from 19 different hermaphrodites

in family 08119. This series of experiments, like those under case III, was calculated to discover any genetic differences which

Pedigree no.	Result	Pedigree no.	Result
09133	44♀:20☿:1♂	09154	57♀:26☿
09134	55♀:27☿	09155	48♀:42☿
09135	41♀:37☿	09156	54♀:41☿
09136	42♀:31☿	09157	56♀:32☿
09137	47♀:33☿	09158	59♀:25☿
09138	47♀:37☿	09159	51♀:29☿
09139	50♀:29☿	09160	43♀:29☿
09140	65♀:25☿	09161	52♀:29☿
09141	38♀:34☿	09162	25♀:30☿
09142	51♀:40☿	09163	56♀:33☿
09149	52♀:25☿:1♂	09164	16♀:14☿
09150	49♀:30☿	09165	46♀:40☿
09151	51♀:45☿	09166	36♀:19☿
09152	66♀:24☿:1♂	09167	36♀:19☿
09153	49♀:22☿		
		Total	1382♀:867☿:3♂

might exist among F_2 hermaphrodites, and the fact that these 29 different individuals when crossed with a single female produced

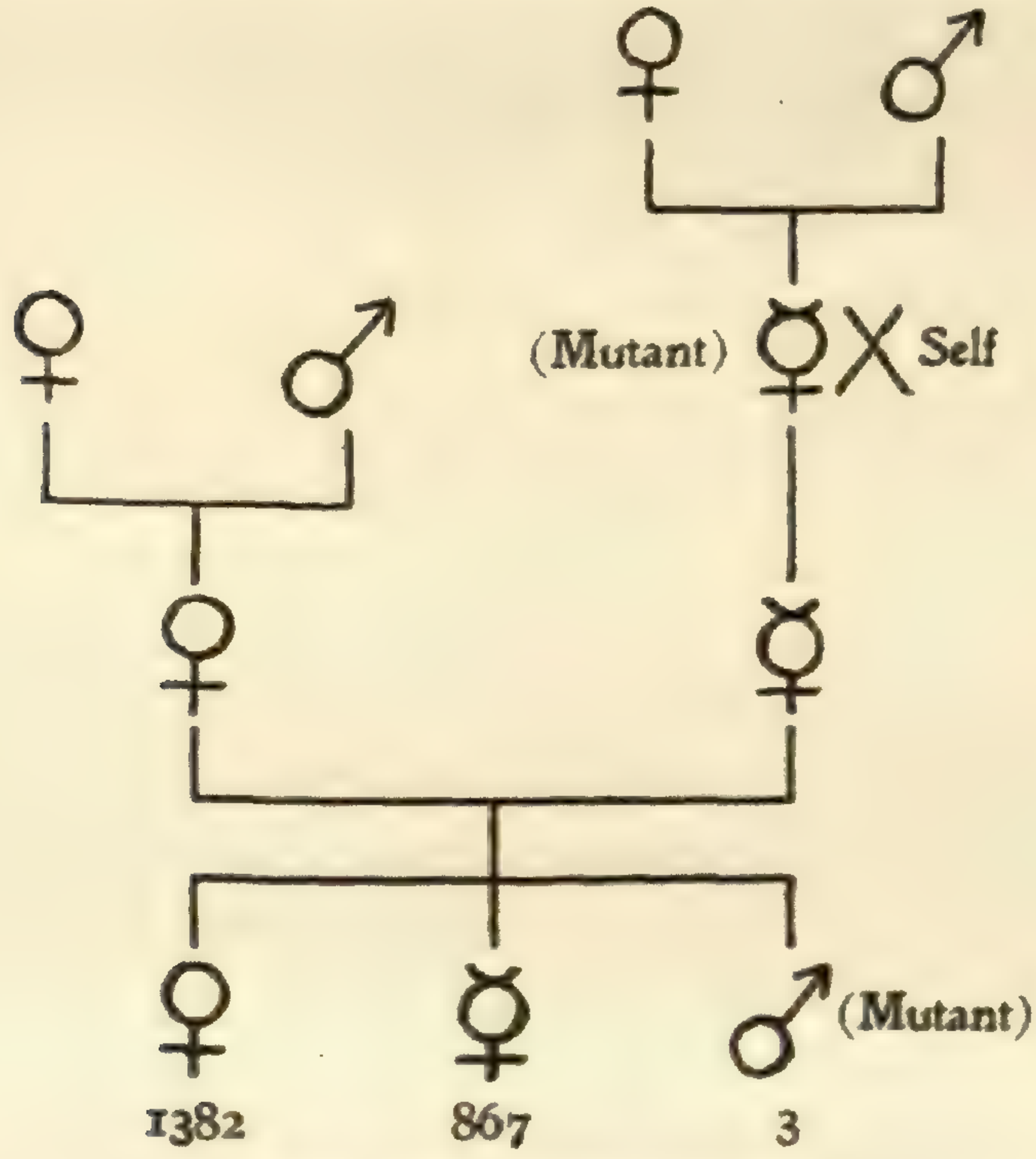

FIG. 4.—Model pedigree for case IV

essentially identical results leads to the conclusion that no such genetic differences existed. This conclusion is apparently open to

but one criticism; the characters of the female chosen to be the mother of all these families might dominate such different characters as were possessed by the hermaphrodites, in which case all families would show identical composition regardless of the variations in the pollen parents. This suggested dominating influence of the female is rendered untenable, however, by the fact that the same female was pollinated by 7 other hermaphrodites having different histories from those considered under the present case, and also by 11 different males of diverse origin, and in every case the males among the progenies were of the same type as their pollen parent.

CASE V

WHEN FEMALE OFFSPRING OF SELF-FERTILIZED HERMAPHRODITES ARE CROSSED WITH AN UNRELATED MALE

Pedigree no.	Result	Pedigree no.	Result
09174	21♀: 8♂	09190	49♀: 22♂
09176	50♀:34♂	09193	28♀: 25♂:1☿
09178	34♀:20♂:1☿	09196	33♀: 23♂
09180	39♀:11♂	09198	58♀: 34♂
09182	36♀:17♂	09200	26♀: 22♂
09184	42♀:34♂:2☿	09202	22♀: 17♂
09189	12♀: 6♂	09204	21♀: 32♂
		Total	471♀:305♂:4☿

These families were produced by pollinating 14 different females, taken consecutively in 08115, with pollen from a single normal male, 0855(36), in an unrelated family. The essentially equal results of all these crosses indicate that there are no differences among these females which were not dominated by the sex character of the pollen parent. As this pollen parent was a male from a normal male parentage, it may be appropriately assumed to have been free from any hypothetically possible hermaphrodite modifier *H*. If such a modifier had been possessed by any of these 14 females, a more striking evidence of that fact should be presented than is found in the occurrence of less than 1 per cent of hermaphrodite individuals among the offspring. This is a smaller percentage of hermaphrodites than has been found in one or two cases among the offspring of a female pollinated by a normal male, neither

parent having had any hermaphrodite connections. It appears fair, therefore, to consider these four hermaphrodites simply as mutants, and not as genetic derivatives from their maternal grandfather. The few hermaphrodites occurring in the families included under the present case may be related to the fact, however, that the females belong to a hermaphrodite family, for the same male 0855(36) was crossed with seven other females and with one hermaphrodite, and among the 443 offspring produced there were no other hermaphrodites.

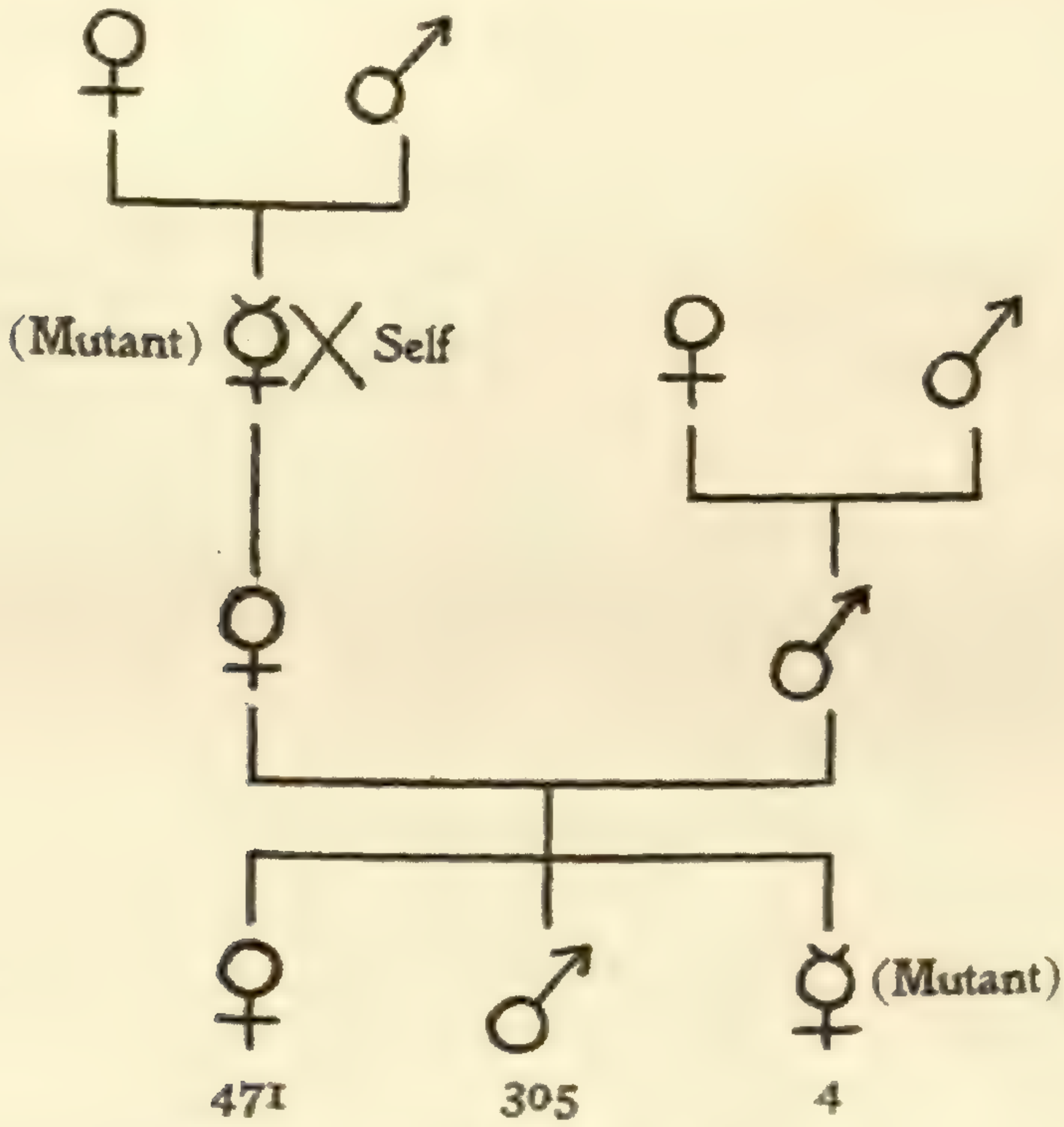

FIG. 5.—Model pedigree for case V

Allowing for the same frequency of occurrence of hermaphrodites as shown in the table above, there should have appeared among these 443 individuals derived from the same male crossed with other females at least two hermaphrodite mutants. This number is so small that they may possibly have been omitted through the errors of random sampling, but the suggestion may be made that while a female cannot transmit hermaphroditism to its offspring, it may perhaps supply an intracellular environment favorable to the mutation of the male genes into hermaphrodite genes.

CASE VI

WHEN THE DAUGHTERS OF A SELF-FERTILIZED HERMAPHRODITE ARE CROSSED WITH ONE OF THEIR HERMAPHRODITE SIBS

Pedigree no.	Result	Pedigree no.	Result
09173	6♀: 2♀	09192	9♀: 2♀
09175	23♀:13♀	09195	39♀:17♀
09177	32♀:17♀	09197	48♀: 6♀
09179	45♀:28♀	09199	40♀:20♀
09181	63♀:16♀	09201	40♀: 7♀
09183	4♀: 3♀	09203	35♀:10♀
09188	36♀: 7♀	09205	9♀: 7♀
		Total	429♀:155♀

The seed parents of these families were the same 14 females which produced the families considered under case V. In the present case they were all pollinated by a single hermaphrodite, 08115(9), in the family to which they themselves belonged. The results correspond closely with those of the last section, except that in this case the males were invariably hermaphrodites, showing as before that the character of the pollen parent determines the sex character of the male offspring. It may be noted that most of these families contained a strikingly high percentage of females, as compared with those under case V, there being 73.46 per cent of females among the progenies of case VI, and only 60.7 per cent among those of case V. The meaning of such differences in the sex ratios is quite unknown at the present time, and no discussion of the series of experiments which are in progress for the purpose of finding an interpretation of such variable ratios will be undertaken here. It is believed, however, that the question of the sex-ratios constitutes an altogether different problem, and has no direct bearing upon matters relative to the genetic interrelationships of the different sexual types, which are alone under consideration in this paper.

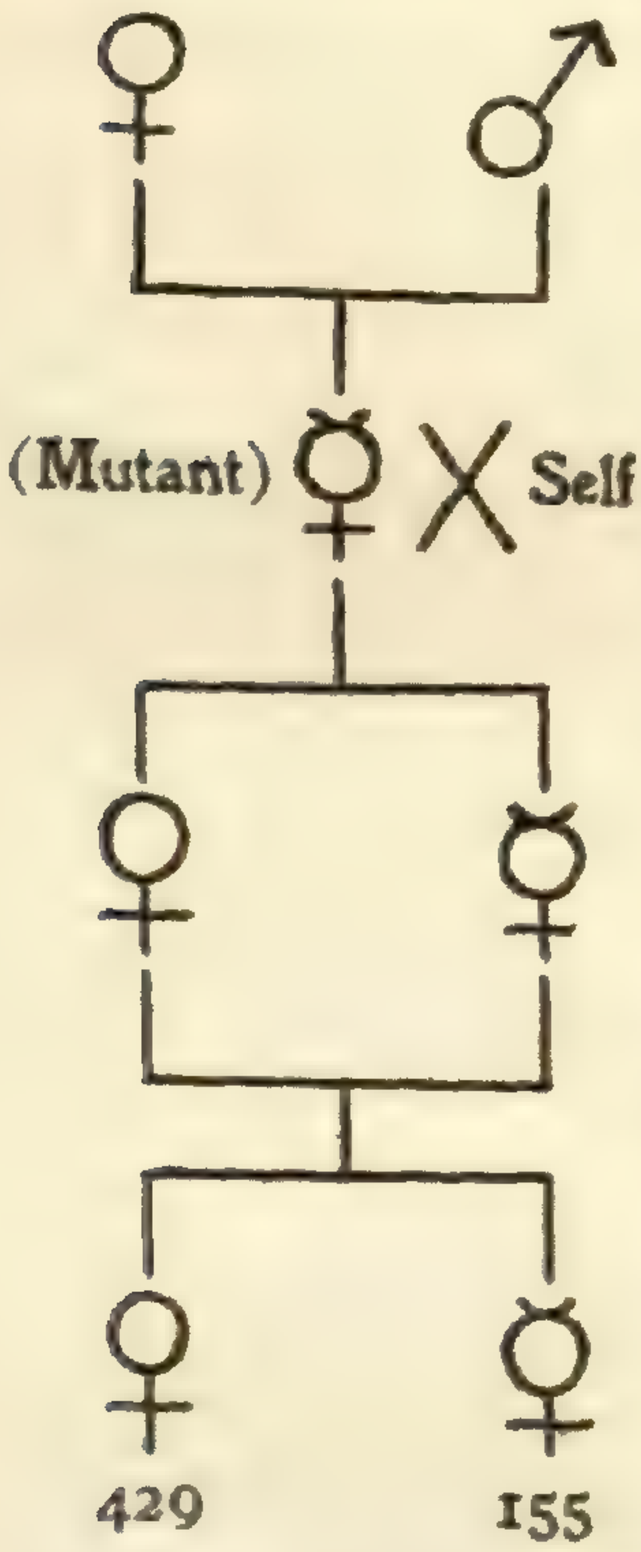

FIG. 6.—Model pedigree for case VI.

CASE VII

WHEN HERMAPHRODITE OFFSPRING OF AN OUT-CROSSED HERMAPHRODITE MUTANT ARE CROSSED WITH UNRELATED FEMALES

Pedigree no.	Result	Pedigree no.	Result
09112	36♀:18☿:1♂	09118	46♀:42☿
09113	56♀:31☿	09145	46♀:49☿
09114	7♀: 3☿	09146	50♀:39☿
09115	20♀:14☿	09148	55♀:24☿
09116	39♀:26☿	09260	26♀:27☿
09117	47♀:19☿	Total	428♀:292☿:1♂

These families are essentially similar in nature to those considered under case IV, except that in the present case the mutant was crossed with an unrelated female instead of being self-fertilized. The first 7 of these families were produced by crossing 7 different

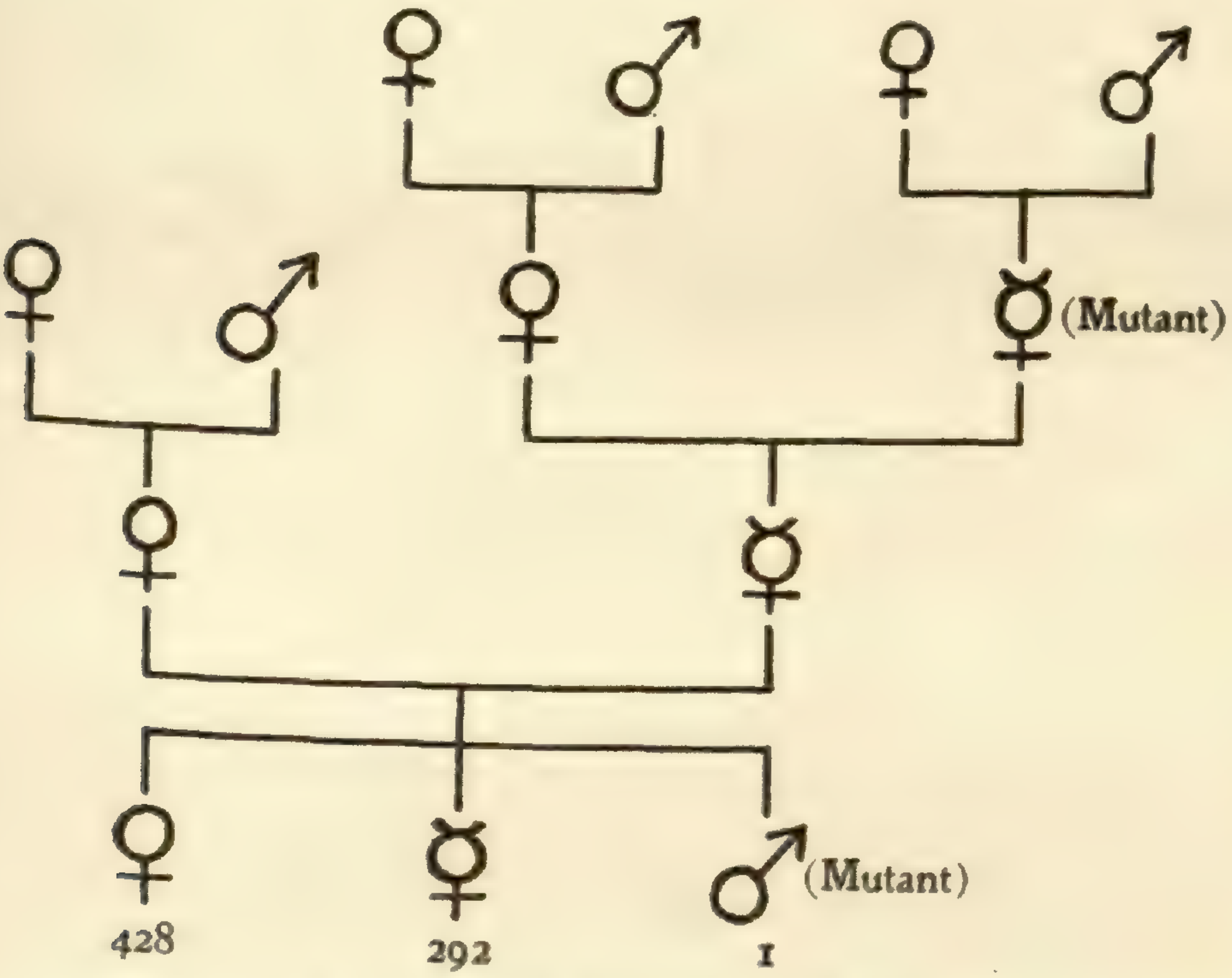

FIG. 7.—Model pedigree for case VII

hermaphrodites in 08118, upon a single female, 08109(1); the next three (09145–09148) were the result of using three of the same hermaphrodite individuals in the pollination of the female, 08114(4), which was used as the seed parent of all the families included under

case IV. The genetic equivalence of the different hermaphrodites again stands out clearly in these results, and when the ratios of the two series are compared, it is found that the percentage of hermaphrodites produced by the hermaphrodite offspring of a self-fertilized hermaphrodite is slightly lower than that produced by the offspring of these cross-bred hermaphrodites, the former producing only 38.2 per cent of hermaphrodites and the latter 42.6 per cent. The difference is too small to be of significance, particularly in view of the fact that much wider differences than this are found in families produced from different seed capsules on a single plant when pollinated by a single male. It might have been expected, perhaps, that a self-fertilized hermaphrodite would have produced a larger percentage of hermaphrodites than would be produced by the same hermaphrodite crossed upon a female of a normal family. The fact that such a result does not appear is further proof that, although the hermaphrodite is a heterozygote, its egg cells are of a single type and like those of the normal females.

The last family under this section was produced by crossing a hermaphrodite of 08128(16) upon a female in a genotypically distinct strain of *Lychnis dioica*, received several years ago from the vicinity of Harrisburg, Pennsylvania. The result is quite the same as in the other families, all of which were derived from a common stock secured at Cold Spring Harbor, Long Island.

CASE VIII

When hermaphrodites are pollinated by normal males

Pedigree no.	Result
08116	21♀:11♂:2☿
09215	8♀: 1♂
Total	29♀:12♂:2☿

I have already remarked the difficulties encountered in the use of hermaphrodites as self-fertilized seed parents. The difficulties are still greater when the problem requires the crossing of the hermaphrodites with other males, for nearly all the numerous castrations which have been made have resulted in the dropping

of the flowers without further development. Only one family (08116) was produced in 1909 from a cross of this kind. It was

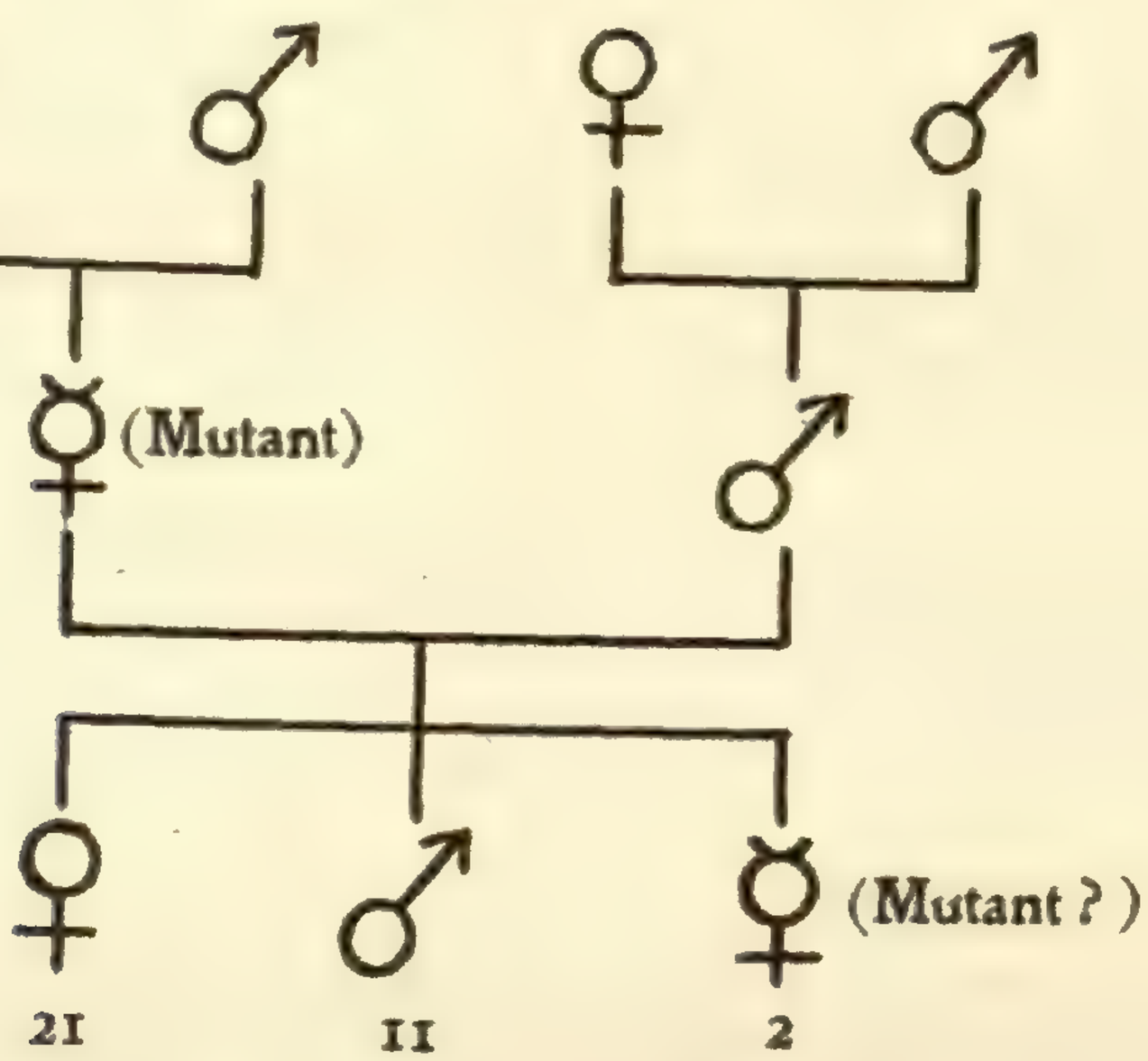

FIG. 8.—First model pedigree for case VIII

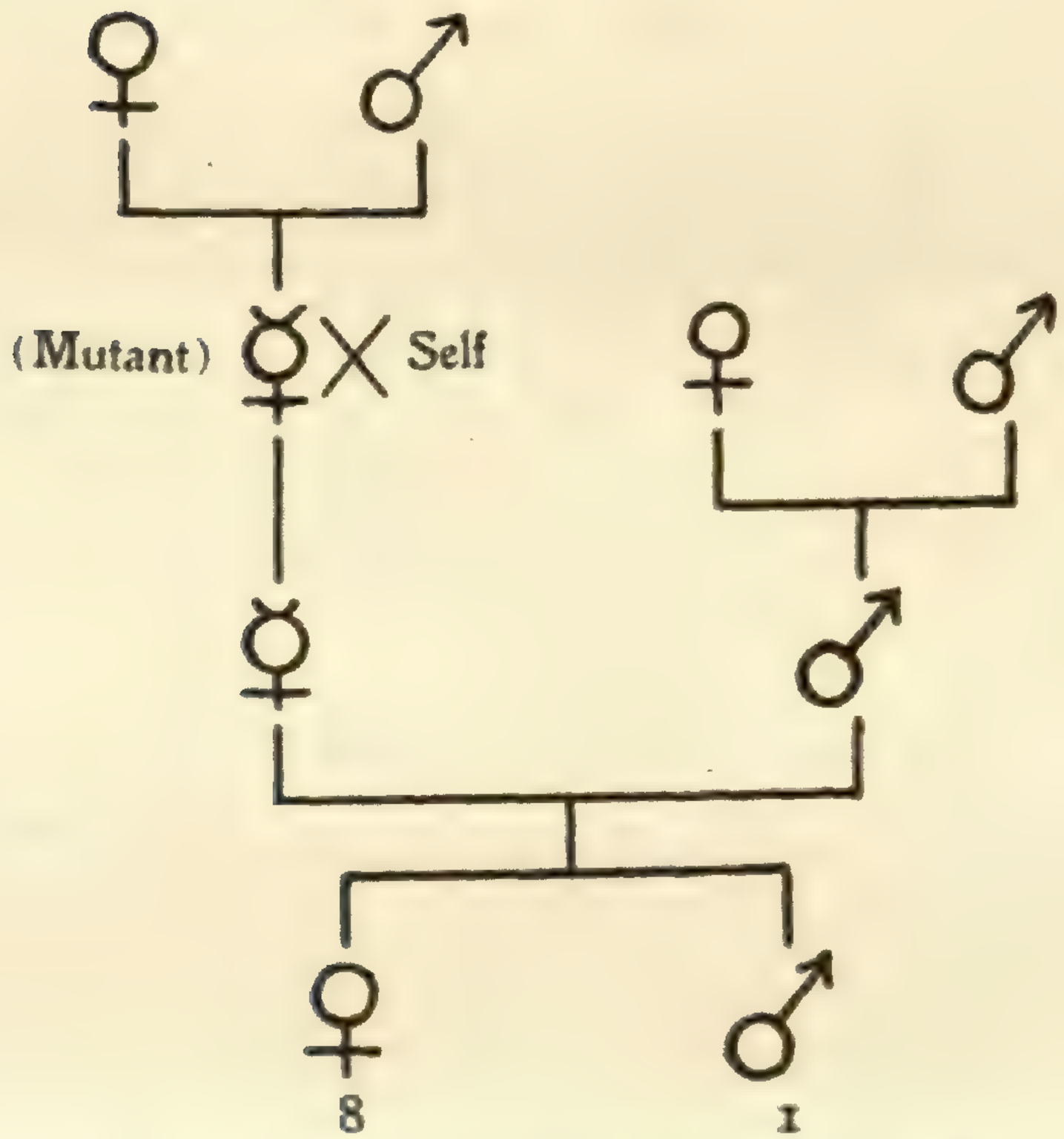

FIG. 9.—Second model pedigree for case VIII

reported upon in my preliminary paper, and is repeated here. The occurrence of two hermaphrodites in this small family suggested that the hermaphrodite character might be inherited from the

mother as well as the father. On this account the cross between hermaphrodites and males must be considered the most important of all combinations in interpreting the relations of the sexes. The difficulty involved in the castration of the flowers permits the question whether the two hermaphrodites may not have been due to a faulty technique, for males produced from unintentional self-pollinations would be hermaphrodites.[3] Special efforts were put forth in 1909 to secure more crosses of this character, but these resulted in a single success, and that of so limited extent as to be wholly indecisive. The 9 offspring of this cross (09215) consisted of 8 females and 1 male, so that the little evidence which such a small family can give is in harmony with the proposition that the character of the female parent has no influence upon the sex characters of the male offspring, except possibly by supplying an intracellular environment which is favorable or unfavorable to the occurrence of sex mutation, suggested under case V. Continued efforts are being made to secure more data from combinations of hermaphrodites with normal males.

CASE IX

WHEN HERMAPHRODITE OFFSPRING OF A HERMAPHRODITE MOTHER AND NORMAL MALE FATHER ARE CROSSED UPON AN UNRELATED FEMALE

Pedigree no.	Result
09143	38♀:38☿
09144	51♀:33☿
Total	89♀:71☿

The appearance of 2 hermaphrodites in family 08116 of case VIII immediately raised the question whether they were true genetic hermaphrodites like *A* and *B*, or whether they might not be somatic hermaphrodites whose hermaphrodite character was not in any way related to the fact that they were the offspring of a hermaphrodite seed parent. If they should prove to be somatic

[3] In a family grown in 1911 from a cross between a white-flowered hermaphrodite and a homozygous blue-flowered male, all the offspring were blue-flowered and several (less than 6 per cent) were hermaphrodite, thus showing that such hermaphrodites are not in this instance due to any unintentional self-fertilization.

hermaphrodites, they would be in reality of the same genotype as their pollen parent, thus offering no exception to the general rule that the male parent determines the sexual type of its male offspring.

Both of these hermaphrodites were crossed upon female 08114(4), already mentioned in cases IV and VII. No influence of the male grandparent appears, as all of the male offspring in these two

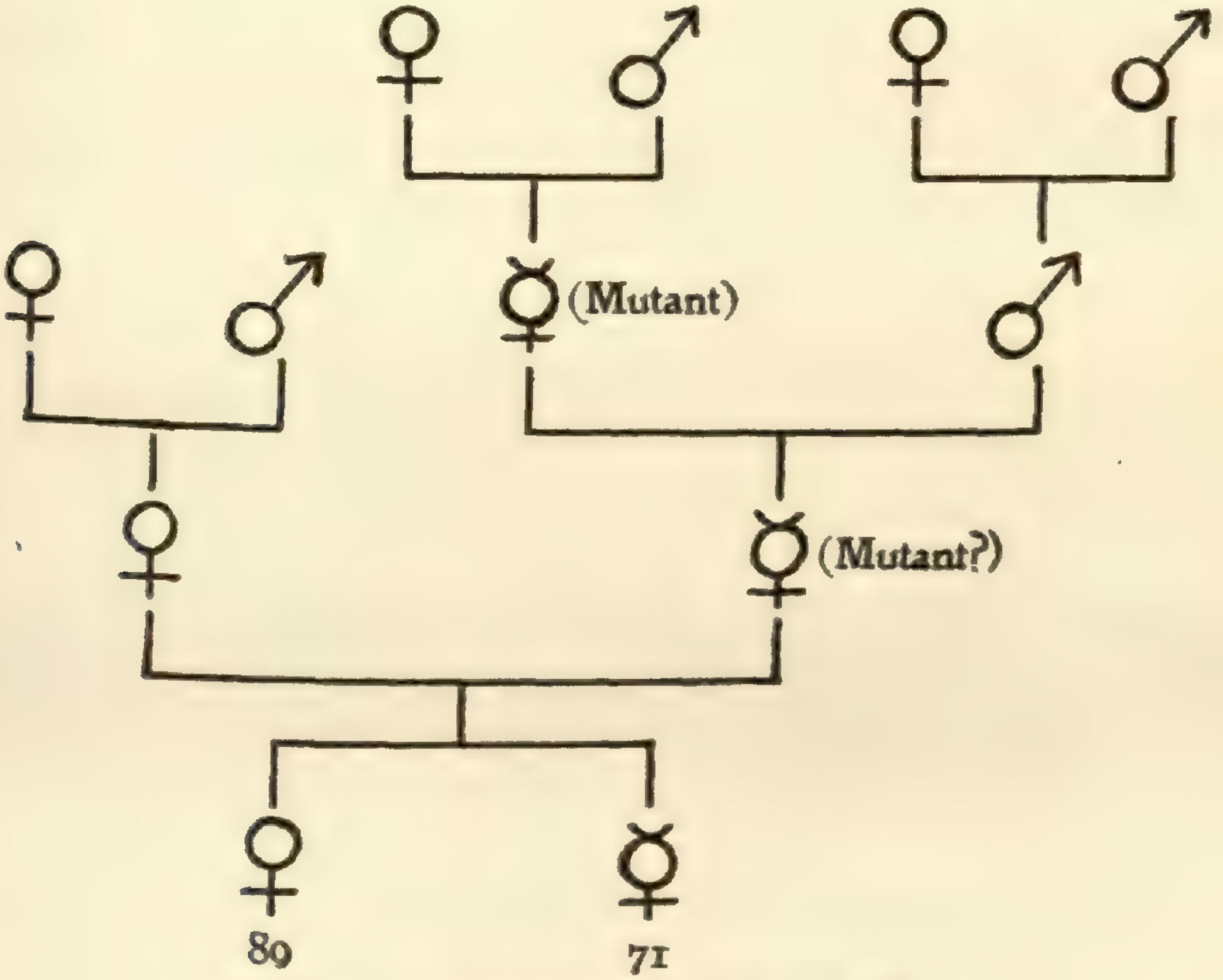

FIG. 10.—Model pedigree for case IX

families were hermaphrodites. This result proves that the 2 hermaphrodites of 08116 were genetic hermaphrodites. One of these hermaphrodites was also self-fertilized and gave a progeny of a single hermaphrodite, constituting family number 09210. It would be rash to draw a conclusion from a family consisting of a single individual, and nothing could have been derived from it if by chance that individual had been a female. The fact that it was hermaphrodite instead of normal male, however, confirms the conclusion that the hermaphrodite parent was a genetic hermaphrodite like its own seed parent.

Whether these two hermaphrodites owed their hermaphrodite character directly to their hermaphrodite mother, or whether it

resulted from a mutation of the male genes received from their father, cannot be definitely decided, but further experiments are in progress to test the possibility that the eggs of hermaphrodites can carry hermaphroditism and may therefore sometimes transmit it to their offspring. The evidence thus far is against their doing so to any considerable extent.

CASE X

CROSSES BETWEEN FEMALES AND THEIR HERMAPHRODITE SIBS IN A FAMILY PRODUCED BY CROSSING HERMAPHRODITE AND MALE

Pedigree no.	Result
09207	1♀: 1☿
09208	12♀: 9☿:1♂
09209	46♀:30☿:1♂
09211	36♀:17☿
09212	32♀:16☿
Total	127♀:73☿:2♂

These are crosses in which the same 2 hermaphrodites of 08116, discussed in case IX, were used as the pollen parents in crosses with

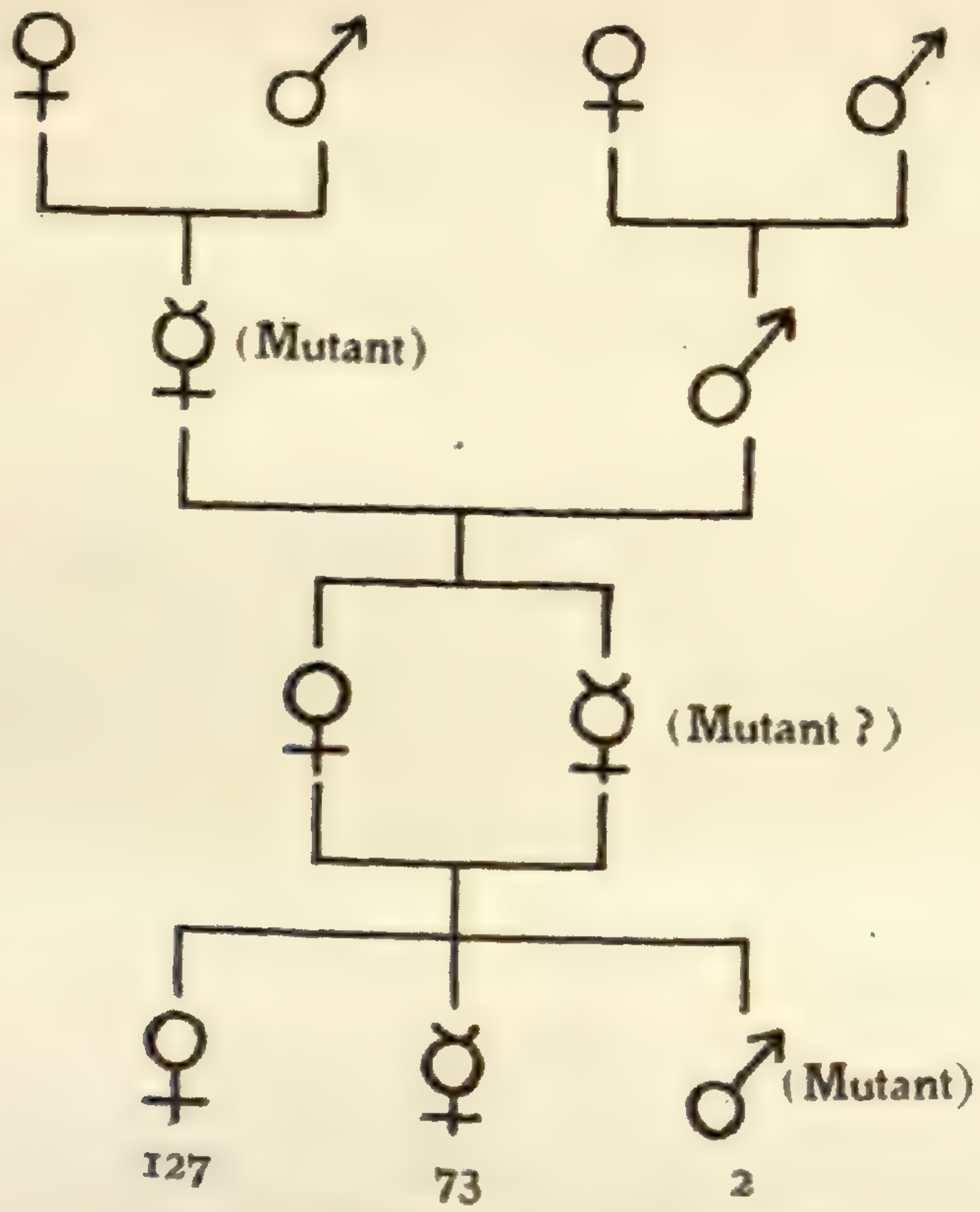

FIG. 11.—Model pedigree for case X

three different females in the same family. The results may be compared with those under case VI, where sib crosses were also dealt with. The comparison shows that the results were identical, though in one case the parents were the progeny of a self-fertilized hermaphrodite, while in the other the parents resulted from the cross of a hermaphrodite fertilized by a male. Thus is given still further evidence that these hermaphrodites in 08116 were genetic hermaphrodites and that such hermaphrodites are of like hereditary capacity, whatever their origin.

CASE XI

WHEN DAUGHTERS OF A HERMAPHRODITE MOTHER AND MALE FATHER ARE CROSSED WITH AN UNRELATED MALE

Pedigree no.	Result
09206	7♀: 5♂
09213	10♀: 8♂
09214	33♀: 21♂
Total	50♀: 34♂

The first of these families (09206) had the same seed parent as the first two families (09207 and 09208) under case X, and the

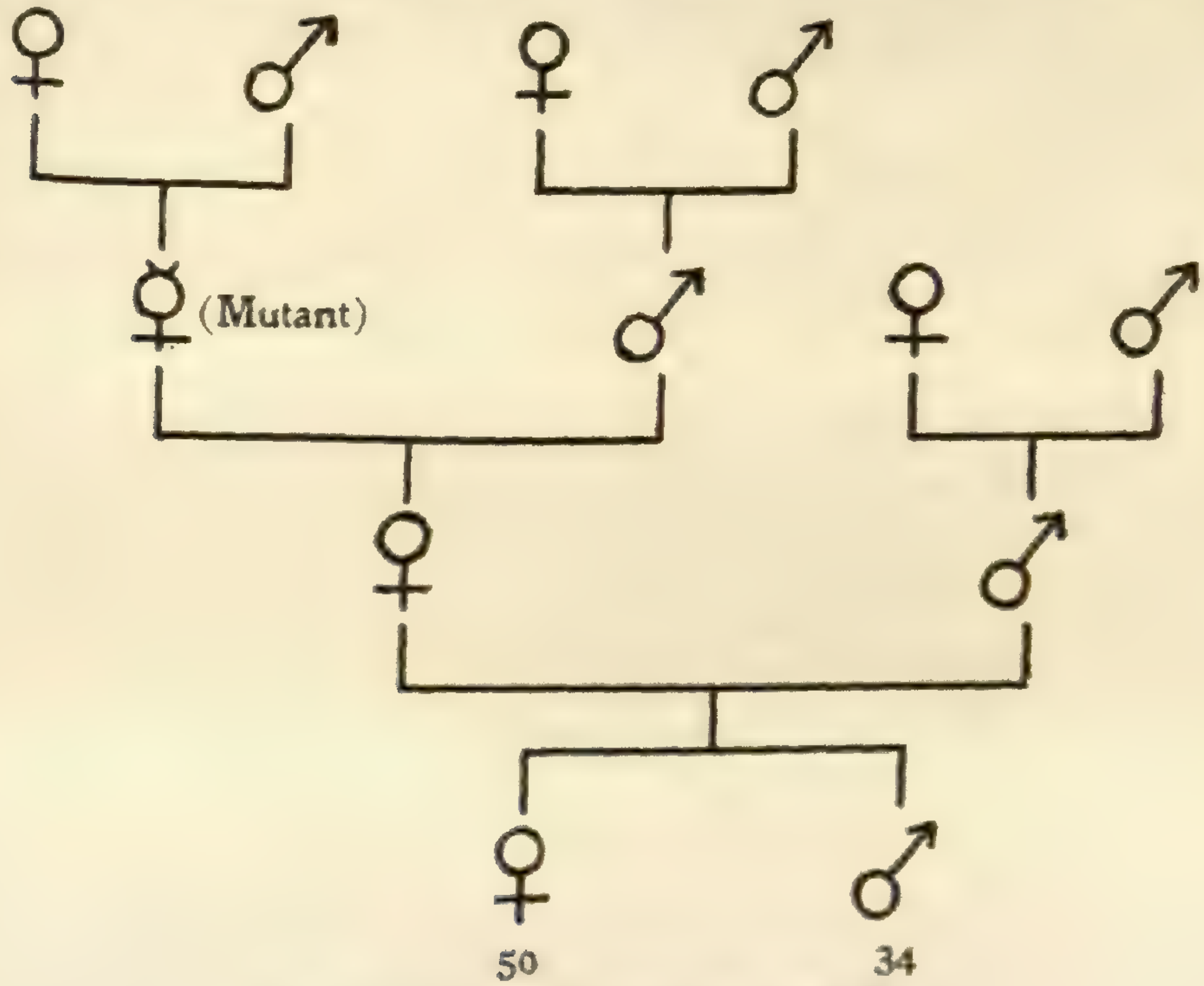

FIG. 12.—Model pedigree for case XI

second (09213) had the same seed parent as the last two families (09211 and 09212) under that case. The pollen parent in all three families of the present case was the same normal male, 0855(36), that was used for all the crosses in case V. It is consequently fair to assume that the differences in the result under case X and case XI are wholly referable to the male parent, and that such differences as appear between case X and case V are referable to the seed parents. There is no difference in the latter instance, while the fundamental difference in the former is that in case X the males were hermaphrodite, while in the present case they were normal males, thus showing again the correspondence between the male offspring and their pollen parent.

CASE XII

When male mutants are crossed with unrelated females

Pedigree no.	Result
09147	40♀:40♂
09239	43♀:44♂
Total	83♀:84♂

It will be recalled that among the 705 offspring produced in 1909 from crosses between females and the genetic hermaphrodites, *A* and *B*, there were 2 males and 305 hermaphrodites. In similar manner it will have been noted that in a number of the cultures of 1910 a very small percentage of such males have appeared in families of which the male offspring were generally hermaphrodite. Instances of this kind are noted above, under cases I, III, IV, V, VII, and X. Whether these males were true males or possibly somatically modified hermaphrodites may now be considered.

The families reported under the present case were produced by pollinating two different unrelated females with pollen of 08118(13), one of the two males derived from genetic hermaphrodite fathers in 1909. No hermaphrodites were produced, thus showing that the pollen parent was a true male, and not a hermaphrodite which had suffered the suppression of the female organs because of some purely somatic influence. The frequency of occurrence of such male mutants may be inferred from the fact

that 11 of them appeared among progenies comprising a total of 3331 females and 2126 hermaphrodites. In other words, they constitute about 0.2 per cent of the total progeny of the genetic hermaphrodites when the latter are used as pollen parents. In no single family did more than one such male mutant occur. While these numbers are too small to allow an accurate estimate of the

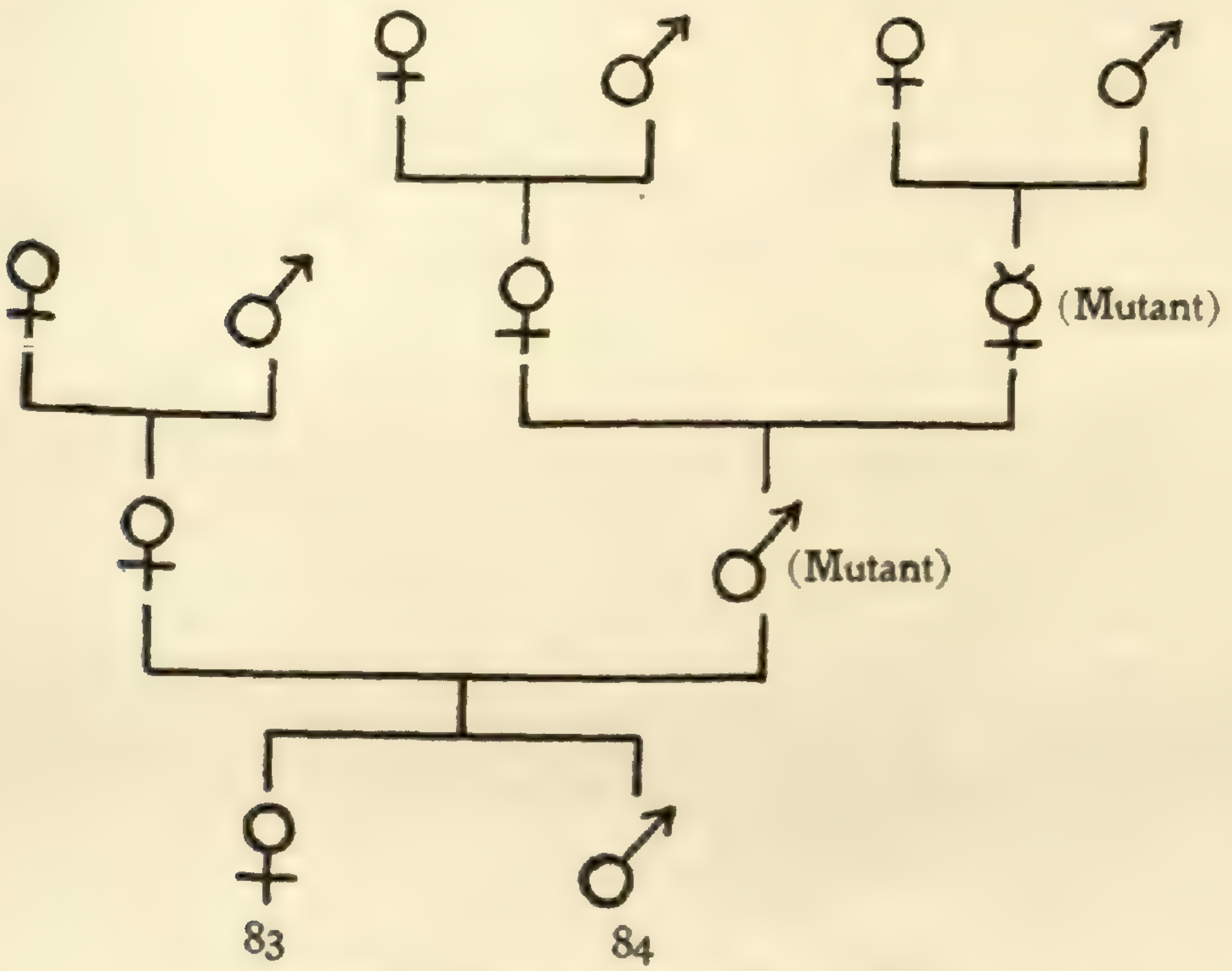

FIG. 13.—Model pedigree for case XII

relative frequency of hermaphrodite and male mutants, the evidence seems to indicate that there is no striking difference between the capacity of males to give rise to hermaphrodite mutants, and that of hermaphrodites to give rise to male mutants, though male mutants have appeared with slightly greater frequency than hermaphrodite mutants.

CASE XIII

WHEN SOMATIC HERMAPHRODITES ARE CROSSED WITH UNRELATED FEMALES

Pedigree no.	Result
08125	39♀:55♂
08132	26♀:18♂
0995	56♀:26♂
0996	63♀:34♂
Total	184♀:133♂

The pedigrees 08125 and 08132 are those of hermaphrodites *C* and *D* among the cultures of 1909, which were reported upon last year. If the "model pedigree" illustrated in the diagram (fig. 14) be compared with that under case I (fig. 1), the two will be seen to correspond perfectly. In fact, the hermaphrodites *A* and *B* included under case I were full sibs of hermaphrodites *C* and *D* whose progenies are repeated here. These 4 hermaphrodites which were found in the cultures of 1908 were indistinguishable

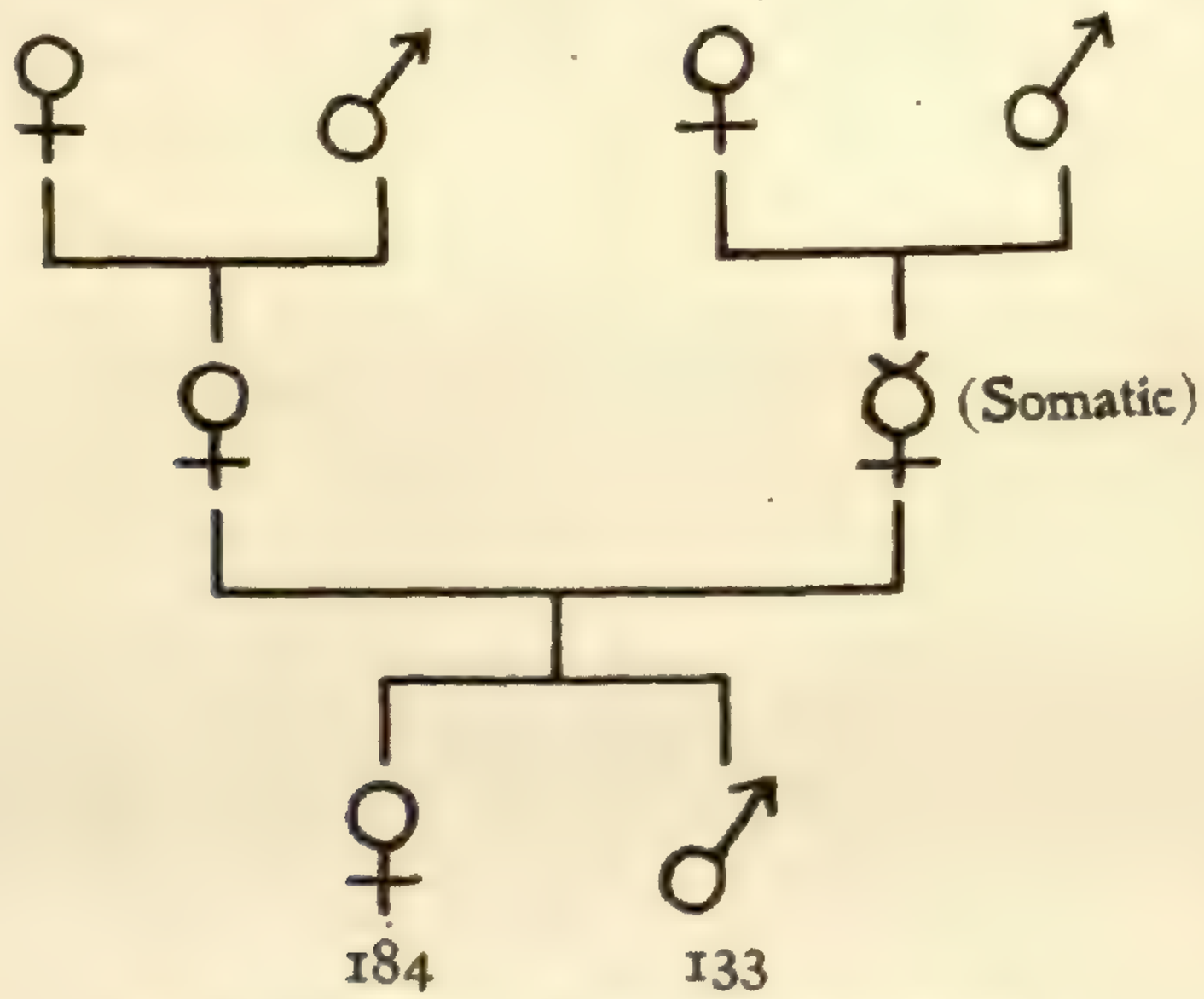

FIG. 14.—Model pedigree for case XIII

from one another in their external characters, and the fact that they belonged in two different categories was only demonstrated by the breeding tests.

No additional instances have been found in which a hermaphrodite indistinguishable from the usual type of "genetic hermaphrodites" has proved to be simply a somatic variation of the male. However, 2 peculiar variant individuals found in one family of the 1909 cultures exhibited an analogous behavior, and consequently their progenies have been added to those of *C* and *D* under this case. The 2 individuals used as pollen parents of the families 0995 and 0996 had several lobes of the calyx prolonged and modified to the form and structure of stigmas, and one of the flowers had in the center a small unicarpellary ovary with an apparently functional stigma. Both of these plants had func-

tional stamens, and both approached more nearly to the type of normal males as the season advanced. On account of the anomalous position of the stigmas in these plants, they are not to be included in the same class with the other hermaphrodites which have been considered, but it may not be unfair to accept the appearance of stigmatic calyx teeth in these male plants as additional evidence that the male is heterozygous in regard to sex, but normally has the presence of the female character completely hidden by the dominance of the male character. A somatic derangement may be assumed as the proximate cause of the appearance of the misplaced stigmas.

These 2 abnormal plants were crossed upon a female sib, 08109(1), and produced together 119 females and 60 normal males, not one of which showed any development of stigmatic calyx lobes or other female characteristics. The female 08109(1) was the one used in case VII for a number of crosses with genetic hermaphrodites, and it was also used as the seed parent in 20 crosses with males of various origin. In all of the other crosses upon this female, the males among the progenies were of the same type as the male parent used in the particular cross from which they sprang, thus showing that this female exerted no modifying influence upon the sex character of her male offspring. This makes it reasonable to conclude that the stigmatic calyx lobes were a purely somatic variation.

CASE XIV

The second generation from a somatic male

Pedigree no.	Result
09119	50♀:27♂
09120	37♀:16♂
09121	33♀:26♂
09122	61♀:14♂
09168	49♀:42♂
09169	45♀:10♂
09170	58♀:33♂
Total	333♀:168♂

In order to make sure that the conclusions drawn from the first generation regarding the character of the hermaphrodites *C* and *D*,

as discussed in case XII, were sound, and that there was not simply the temporary disappearance of the hermaphrodite character through some thinkable vagary of dominance in the F_1, 5 males in 08125 were tested in crosses with 2 different females. The resultant progenies consisted of 333 females and 168 males. Not a single hermaphrodite appeared, thus convincingly supporting

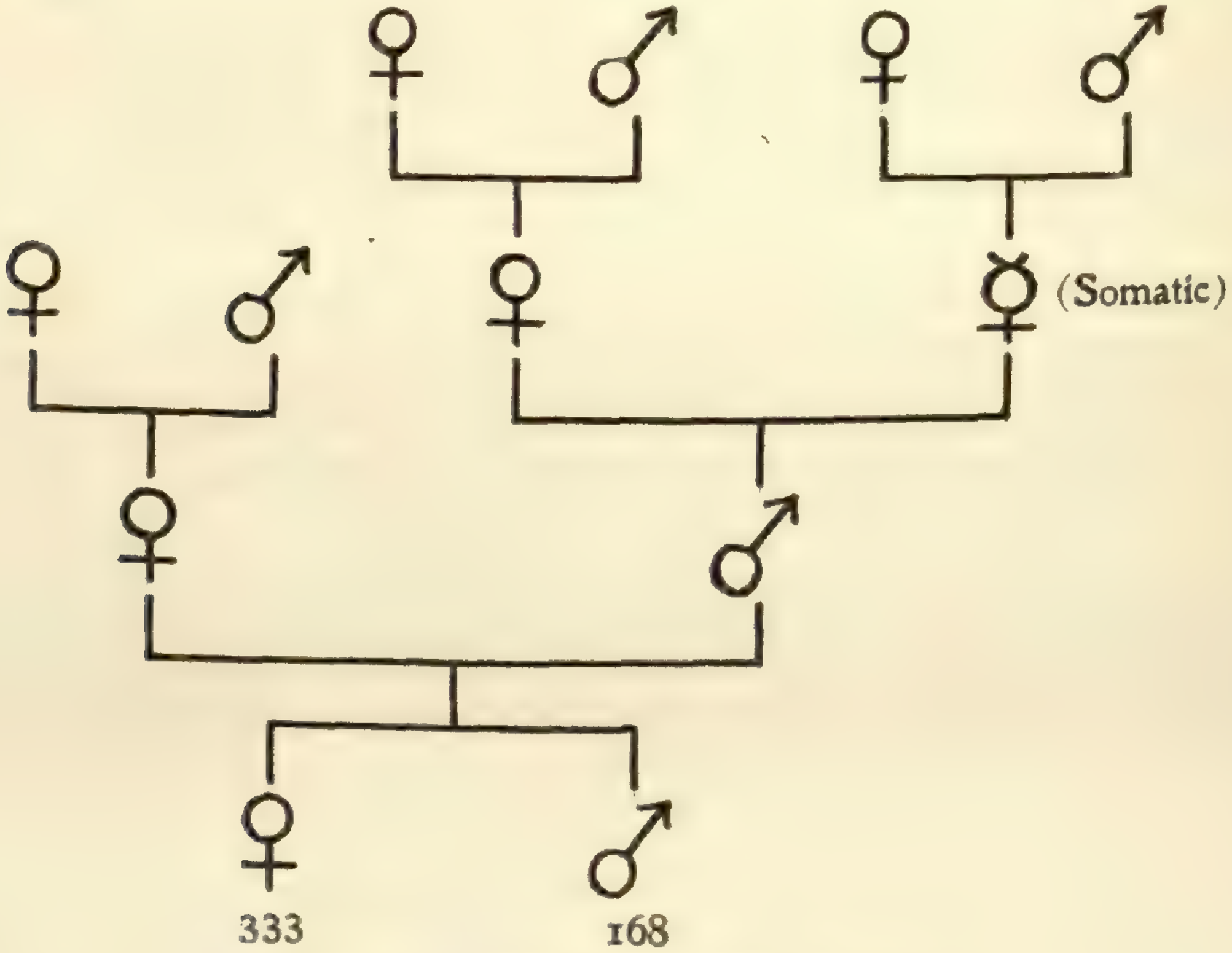

FIG. 15.—Model pedigree for case XIV

the view that the appearance of hermaphroditism in *C* and *D* was illusive, and that they were therefore only superficially like the genetic hermaphrodites *A* and *B*. These results fully justify my conclusion that the hermaphrodites of *Lychnis dioica* belong to two genotypes, one of which is the same as the normal male, the other different from it.

Discussion and conclusions

Although these data from the breeding of hermaphrodites of *Lychnis dioica* are presented in fourteen sections, each representing a somewhat different direction of attack upon the genetic problems involved, the results under the various sections are remarkably consistent. The hermaphrodites are clearly of two kinds. Those

included under cases I–XII produced male offspring like themselves when they were used as male parents (but not when used as female parents). These have been called "genetic hermaphrodites," to distinguish them from occasional genetic males which possess female organs as a purely somatic modification, and which I have therefore called "somatic hermaphrodites." These "somatic hermaphrodites" will be omitted from the discussion for the present.

Under cases II and III it is shown that genetic hermaphrodites, of whatever origin, when self-fertilized, yield dimorphic progenies consisting of females and hermaphrodites, thus confirming the conclusions derived from the F_1. This fact, together with the apparent relative ease with which males are made to exhibit the organs of both sexes, has been accepted as conclusive evidence that the hermaphrodites (and therefore also the males) are heterozygous with respect to sex, and the females homozygous (SHULL **26**). In this regard *Lychnis dioica* L. agrees with *Bryonia dioica* (CORRENS **6**); with many species of Coleoptera, Orthoptera, Hemiptera, Diptera, Odonata, and perhaps also with Myriapoda and Arachnida (MCCLUNG **19**, WILSON **38–42**, MORGAN **20, 21**, STEVENS **31–34**, etc.); and with the nematode worms, *Heterakis* (BOVERI **4**) and *Ascaris megalocephala* (BORING **3**). In man, GUYER (**16**) has demonstrated that there are two types of sperms, and while the relation of one or other of these types to the type of the egg is unknown, there can hardly be a doubt that here also the female is homozygous and the male heterozygous.[4]

Although these widely divergent groups of plants and animals agree in having homozygous females and heterozygous males, there may still be fundamental differences in the different groups, since there may be three different kinds of homozygotes, and correspondingly different kinds of heterozygotes. This question

[4] Heterozygous females have now been recognized in *Abraxas* (DONCASTER and RAYNOR **10**, and DONCASTER **8, 9**), sea urchins (BALTZER **1**), canaries (DURHAM and MARRYAT **11**), and in domestic fowl (BATESON **2**, SPILLMAN **28, 29**, GOODALE **12, 13**, HAGEDOORN **17**, PEARL and SURFACE **24, 25**, STURTEVANT **37**). GUYER (**14, 15**) reports two types of sperms in both the guinea fowl and the common fowl, but these observations are out of harmony with all the genetic studies in which sex-limited characters of the Gallinaceae have been involved. The considerable difficulties encountered in the cytological studies on these species suggest the advisability of a repetition of this work.

will be discussed later in connection with the nature of the hermaphrodites.

CORRENS (**6,** p. 17), with undoubted justification, maintained that the germ cells of monoecious, hermaphrodite, and dioecious species possess the tendency to develop into individuals having the distribution of sex organs characteristic of the particular genotype to which they belong; but when he likens the association of organs of both sexes in the same individual to the mosaic of red and white colors in striped flowers, and of pigmented and white spots in the coats of spotted animals, his justification becomes less obvious. Both striped flowers and spotted pelages are known from many investigations to be due to the presence or absence of a definite Mendelian gene, a so-called "spotting factor" or "pattern factor."

One of the chief aims in the arrangement of my cultures for 1910 was to test the possible existence of such a mosaic or "pattern factor," *H*, as a proximate cause of hermaphroditism in *Lychnis*, and the most striking result secured is the decisive manner in which such a possibility is denied. The hermaphrodite character is not only incapable of reaching expression in the female[5] (as might be expected, since the female is homozygous), but it is also as a rule not transmitted through the egg cell to the male offspring. The males in the progeny of any cross agree in their sexual type with the male parent of that cross, regardless of its antedecent history. All the assumptions and implications involved in the first section of table I, in which an independent gene *H* was postulated, may therefore be rejected.

[5] I refer here only to the normal functional hermaphroditism with which this paper deals, and not the pseudo-hermaphroditism which results when females of *Lychnis dioica* are attacked by the smut, *Ustilago violacea*, as reported by STRASBURGER (**35**). I was inclined (SHULL **26**) to consider STRASBURGER'S interpretation of the effect of *Ustilago* a mistake, as it appeared to me more probable that the infected plants were males whose heterozygous nature easily permitted the development of the female characters. STRASBURGER (**36**) has shown conclusively, however, by two series of facts, that his original observations and interpretation were correct. These facts are (*a*) that diseased plants are not always completely infected, in which case the uninfected branches of the pseudo-hermaphrodites have normal female flowers; and (*b*) that male plants may be infected also, but such infection does not in this case result in the development of the female organs.

In the second section of table I the hypothetical gene *H* for hermaphroditism is given limitations which make it fit all the empirical results of both the first and subsequent generations; but when the significance of the limitations is taken into account, it becomes evident that there is small advantage gained by the postulation of such a gene. Indeed the only advantage lies in the fact that in case the female is a positive homozygote, it keeps open the question whether or not there is a synaptic mate of *F* in the normal male; for a newly arisen hermaphrodite gene (*H*) might conceivably become a synaptic mate of *F*, even though the latter had had no synaptic mate in the normal male.

If the female is a neutral homozygote, that is, if the female gene *F* has a male gene *M* as its synaptic mate in the male, the hermaphrodite gene (if it exist at all) must be absolutely coupled with this male gene. In like manner, if the female is a negative homozygote *FFmm*, the *H* (if present) must be coupled with the male gene *M*. It is simpler, however, to assume that the hermaphrodite determiner is a modified form of the sex gene itself, than to suppose that it is a separate gene invariably coupled with the sex gene. This conception that hermaphroditism results from a mutative change in the sex gene, or in its homologue (?), the "Y-element," is made the basis of the last section of table I, but can apply only to those cases in which a male gene is present, or if not a male gene, then its homologue, a sexually indifferent gene which takes the place of *M* in the male; for if the hermaphrodite character is assumed to be due to a change in the female gene (*F*), as it must be if the latter has no "synaptic mate," the scheme will not work.

It appears to me impossible at the present time to determine whether the females of *Lychnis* are positive, neutral, or negative homozygotes. The facts seem to be equally well met by any of these assumptions; but the definite limitations of the hermaphrodite character to the males makes inapplicable the extreme form of the "presence and absence" hypothesis (that is, the hypothesis of unpaired genes) unless the female is a negative homozygote with reference to a male sex gene (*M*). While the possibility must be kept open that this is the relationship of the sexes in *Lychnis*,

it seems to me more probable that the female is a neutral homozygote (*FF*), the male having the formula *FM*, and the hermaphrodite the formula FM_H. The gradually increasing number of known instances of "spurious allelomorphism" proves that the pairing of unlike or unequal genes in the heterozygote is, if not the general condition, at least a not uncommon one.

The question whether the sex genes are paired or unpaired in the heterozygote, and if unpaired, whether the female is a positive or a negative homozygote, might be settled by simple observation, if it could be known that the chromosomes are the sex determiners, as a number of recent cytological studies clearly suggest. It is not at all certain, however, whether the unequal chromosome groups in the male-producing and female-producing germ cells are active *determiners* or simply passive *indicators* of other more fundamental differences. The latter possibility is strongly emphasized by MORGAN (**20**), who shows that the pole to which the accessory chromosome in *Phylloxera* is to proceed, is already determined before that chromosome has given any indication, by its own motion, to which pole it will go. This suggests that the poles of the dividing spermacyte may be sexually differentiated in advance by some other factor. If the chromosomes are not the sex-determiners, but only passive indicators, the fact that they are paired or unpaired, equal or unequal, has no decisive bearing upon the question whether the female is a positive, neutral, or negative homozygote, or whether the genes are paired or unpaired in the heterozygote, for it is quite as easy to assume that the movement of the accessory chromosome or "X-element" to the female pole takes place in response to a tension caused by the *absence* of a positive *male* sex-determiner at that pole, as that it is attracted by the *presence* of a positive *female* determiner. If the "X-element" should move into the vacancy caused by the absence of the sex-determiner, the presence of the added chromosome or group of chromosomes would become the evidence of the absence of the sex gene; in other words, the female possessing the added chromosome would be a negative homozygote. All this is highly speculative, and as there appears to be no way as yet to put the matter to experimental test, it seems futile to discuss further the question

whether the female of *Lychnis dioica* is a positive, neutral, or negative homozygote, or whether the synaptic mate of the female gene is qualitatively male or not. The matter has been considered at such length only because it is important that no unwarranted conclusions should be drawn from the configuration of the chromosomes in any given case.

There appears to be no very strong evidence at present that the chromosomes are the representatives or producers of particular Mendelian unit characters, though attempts have been made a number of times during the past decade to identify them as such. On the other hand, there is still no positive and complete demonstration that the chromosomes are *not* the determiners of the Mendelian characters, and until this demonstration is provided, the relation of the chromosomes to the unit characters must be kept open. Whether the chromosomes are responsible directly for sex may well remain likewise an open question for the present, especially in view of the fact that in many animals, and in the few plants which have been thus far investigated, no chromosome differences have been found to differentiate the sexes.

There can be no doubt of course that the sex characters are *associated* with chromosome differences in the considerable number of animals which have been found to present such differences, but, as we have just seen, the nature of this association is not clear. Where two types of sperms are found in the male, the one type corresponding in its chromosome complex with the single type presented by the eggs, the inference is fully justified that such males are heterozygous and the females homozygous in respect to sex, whether one or more chromosomes be the sex-determiner, or whether these chromosomes are merely symptomatic of other fundamental differences which are the true sex-determiners; and vice versa, when two types of eggs having different chromosome groups are found in the female, one of which agrees with the only type found in the sperms, the inference is fair that the female is heterozygous and the male homozygous in respect to sex. So consistent have been the results in those species in which both male and female germ cells have been investigated, that it has not seemed improper to assume that in any given species the one sex will have

uniform germ cells, and is to be considered homozygous, if the other sex is demonstrated to have two types of germ cells.[6]

No chromosome differences have been found in *Lychnis dioica* L. by STRASBURGER (**36**), who has studied a form of this species known in German taxonomic works as *Melandrium rubrum* Garcke. His careful investigation of germ cells and root tips showed 24 chromosomes to be the somatic number, one pair of these chromosomes being notably larger than the rest, thus resembling the accessory chromosomes or supposed sex chromosomes of the insects. However, in *Lychnis*, the two members of this pair are indistinguishable from each other in both the male and the female. The same results have been independently secured by Miss LUTZ during the past year, but have not yet been published. *Lychnis* appears to agree, therefore, with *Nezara*, *Oncopeltus*, etc. (WILSON **39, 40**), among the Hemiptera, as in these the two types of sperms, which doubtless exist, are not visibly differentiated. STRASBURGER (**36**) reports also that an investigation of *Bryonia dioica* has not revealed the two types of sperms that might *a priori* have been expected.

The hypothesis of unpaired determiners implies that a new Mendelian character originates by the formation of a new gene or the loss of an old one. My interpretation of hermaphroditism in *Lychnis dioica* as due to an alteration in a sex gene already in existence, which alteration does not in any way change the homology of the gene in question, calls for a fundamentally different method of origin of new characters from that involved in this extreme form of the "presence and absence" hypothesis. The new genotype which arises by mutation from the old one has in this case neither more nor fewer genes than had the genotype from which it originated.

The occurrence of male mutants among the offspring of my genetic hermaphrodites appears to me to have a bearing upon this question, as to the mode of origin of new characters. Among the offspring of genetic hermaphrodites tabulated in this paper, 11 male mutants appeared, and under case XII it is shown conclusively that these are true males, and do not again give hermaphrodite offspring, except probably in the extremely small proportion given

[6] As already noted, GUYER'S (**14, 15**) studies on spermatogenesis in the domestic fowl and in the guinea fowl appear at present to be exceptions.

by males not derived from a hermaphrodite family. These 11 males appeared in hermaphrodite families comprising a total of 5467 individuals, thus possibly indicating a somewhat greater coefficient of mutability than that reported for the production of hermaphrodites from normal males. It seems therefore that the modification of the gene *M* (or *f*) into a hermaphrodite gene *H*, and the reversal of this modification so that a normal male gene is again produced from a hermaphrodite gene, occurs with somewhat unequal facility, but the difference is not great enough to warrant the belief that mutation in the one direction is caused by the appearance of a new, independent organ, while its reversal is due to the disappearance of that organ. It seems to me more probable that these reversible mutations are due to reversible modifications of an element or organ continuously in existence, and not to the production of a new element or the dropping out of an old one.

The change from a male to a hermaphrodite condition and the reverse are processes both striking and sudden. Perhaps they are as fundamental mutations as those observed among the oenotheras. The interpretation given here of the process of mutation in the sex character of *Lychnis* seems to be available for other mutations as well. The sudden acquirement of new functions by a gene already in existence is different from the conception presented by DE VRIES in *Die Mutationstheorie*, to account for the origin of the *Oenothera* mutants, and is in accord with SPILLMAN'S "teleone hypothesis." SPILLMAN (**30**) is inclined to attribute the remarkable mutations in *Oenothera* to irregularities of mitosis, but in these sex mutants of *Lychnis*, abrupt genotypic modifications have taken place which can hardly be assigned to such irregular mitoses.

One puzzling feature of the inheritance of sex in *Lychnis* is the fact that self-fertilized hermaphrodites produce similar ratios of females and hermaphrodites as are produced when unrelated females are fertilized by sperms from hermaphrodites. Since it is obvious that the two types of offspring are due to the heterozygous character of the male, we are led to the conclusion that even though the hermaphrodite individual is heterozygous in respect to sex, its egg cells[7] are of a single type like those of the normal female

[7] Perhaps I should say "its *successful* egg cells."

and carry only the female tendency, while its sperm cells are of two types, one of which has the same sex character as the egg cells, the other bearing the hermaphrodite condition. In my preliminary paper, it was suggested that those eggs may fail to develop which lack the female gene *F*, or which possess the male gene *M;* or that in case the female is a negative homozygote, there might be an extrusion of the male gene during oogenesis. As there are no visible cytological differences between the females and the hermaphrodites, it may not be possible to decide these questions. The relatively small number of seeds in the hermaphrodites, as compared with the females, appears to be favorable to a selective elimination of male-bearing eggs. Another explanation seems possible. A segregation of the female and male genes may conceivably take place earlier than the time at which the germ cells are formed, though it must be admitted that there is little evidence at present that such early segregations regularly[8] take place in any plant or animal. Such a suggestion has been made by BATESON (**2**, p. 159), however, in the effort to account for certain interesting instances of coupling. If a segregation of female and hermaphrodite genes could be assumed to take place as early as the formation of a certain primordial cell from which the entire reproductive tissue of the ovary develops, so that the ovules are supplied only with the female genes, the observed uniformity of the egg cells would result. If segregation may take place thus before the spermacytes are developed, this might also offer an explanation of the exceedingly variable sex ratios which occur in *Lychnis*, for an unequally rapid development of tissues derived from female-bearing cells and male-bearing cells, from the moment of segregation until the spermacytes are produced, would give an unequal number of female-bearing and male-bearing sperms, and variability in this process would produce irregular ratios. I place no stress upon this hypothesis, however, and am inclined to look for an explanation of the observed phenomena in some sort of selective elimination.

There remains to be considered the relation of the somatic hermaphrodites to the problems of sex determination. The results under cases XIII and XIV show that the hermaphrodite

[8] They are known to take place occasionally in the production of bud sports.

character of these plants was purely superficial and did not affect the germ cells in any recognizable manner. The only bearing these plants have upon the question of sex determination, I think, is in the evidence they give that genetically normal males may be induced in some unknown way to exhibit female characters. When the male is interpreted as a Mendelian heterozygote in respect to the sex-producing gene, the occurrence of such a somatic modification has the appearance of a simple case of imperfect dominance, such as has been noted not infrequently in other Mendelian heterozygotes. However, the development of male organs (non-functional) in the supposedly homozygous female, when the latter is attacked by the smut (*Ustilago violacea*), gives support to the view held by STRASBURGER (**36**), that not only the heterozygous sex but both sexes contain in some degree the elements of the opposite sex or the capacity to react in the sexually opposite manner. This fact may perhaps indicate that sex is a more fundamental condition than might be inferred from the frequency with which it behaves as a Mendelian unit character. MORGAN (**23**) suggests a way in which the appearance of the organs or characters of one sex in individuals of the opposite sex may be explained in harmony with the Mendelian interpretation of sex determination. He assumes that there may be present, underlying the female sex gene, a male element with respect to which all individuals of both sexes are homozygous. This he indicates by introducing *m* into all of his sex formulae. In keeping with common usage among geneticists, he should have used *M*, since he intends to denote the *presence* of maleness.

While recognizing the aptness of this suggestion in removing some of the difficulties in the way of a general application of the Mendelian explanation of sex, I am inclined to the view that the Mendelian nature of sex is of secondary rather than of primary consequence. May not maleness and femaleness be thought of as alternative states, which can be crudely analogized with the acidity and alkalinity of chemical solutions? Just as solutions may be made acid or alkaline in different ways, either by qualitative or by quantitative additions, subtractions, or substitutions, or by a combination of qualitative and quantitative changes, it

is conceivable that the alternative sexual types may be determined in different cases by very different methods, some qualitative, some quantitative, and others both qualitative and quantitative. In some species the sexes appear to represent a much more strongly polarized (?) condition than in other species, and a transition from the characters of the one sex to those of the other is attained only with the greatest rarity, if at all; while in other species the sex conditions may be so nearly balanced or neutral that individuals are not so absolutely determined in their sex relations by their genotypic nature, thus resulting in ever-sporting varieties in respect to sex, such as CORRENS (**7**) has found in *Plantago lanceolata*.

With such a conception of sex, it also appears probable that sex may be influenced sometimes by external factors as well as by internal ones, and in this case the preponderance of one sex over the other, which has been observed in many animals and plants, need not be attributed alone to a selective disorganization of germ cells, a selective fertilization, or a selective death rate, but might conceivably be controlled to a certain extent by environmental conditions acting at some particular "sensitive period" in the ontogeny of the organism in question. However this may be, there is little or no evidence at present that such environmental influences on sex can be more than relatively slight in the case of dioecious plants and animals. In such organisms recent genetic and cytological studies prove conclusively that sex is generally determined by the genotypic nature of the individual.

Summary

The hermaphrodites of *Lychnis dioica* are modified males. They are of two kinds, which are here distinguished as "genetic" and "somatic" hermaphrodites.

When the genetic hermaphrodites are used as pollen parents, either when self-fertilized or in crosses with females, their progenies consist of females and hermaphrodites. When they are used as pistil parents, and fertilized by normal males, they produce females and normal males.

Somatic hermaphrodites may be externally indistinguishable

from the genetic hermaphrodites, but when used as pollen parents they produce no hermaphrodite offspring, but only females and normal males.

The fact that males can be modified so as to produce functional organs of both sexes, indicates that they are sex heterozygotes, and the production of both females and hermaphrodites by self-fertilized hermaphrodites strongly supports the same interpretation.

The hermaphrodite character can neither find expression in the females, nor can it be transmitted by their eggs to the male offspring. Consequently it is not determined by an independent gene, *H*, but by a modification of the male sex gene, *M*, or of the "synaptic mate" of the female gene, *F*.

If the males and hermaphrodites are heterozygous, it follows that the females are homozygous; but this does not offer an ultimate solution to the relationship between females and males, since there may be several different kinds of homozygotes and heterozygotes. As applied to the relation of the sexes, these may be indicated by the following formulae: (*a*) The female may be a "positive" homozygote; then $FF = ♀$, $Ff = ♂$, Ff_H or $FH = ☿$. (*b*) If the female is a "negative" homozygote, $FFmm = ♀$, $FFMm = ♂$, $FFM_Hm = ☿$. (*c*) When the female is a "neutral" homozygote, $FF = ♀$, $FM = ♂$, $FM_H = ☿$. In each of these formulae the subscript *H* is intended to represent a modification of the gene to whose symbol it is appended, such that the male is changed to a hermaphrodite. Which of these formulae correctly represents the condition in *Lychnis* can not be determined, but the modified gene which results in hermaphroditism is allelomorphic to *F* unless the female is a negative homozygote.

Among the offspring of genetic hermaphrodites were a small number of male mutants (11 in 5467), which on breeding proved to be normal males. The occurrence of these male mutants indicates that the modification to the hermaphrodite condition, and back again to the male condition, occurs with but slightly unequal facility, and this circumstance is believed to favor the view that mutation in this case depends upon reversible modifications of some permanent element or organ, rather than upon the origination of a new unit, and its disappearance. This interpretation

bears both upon the nature of mutation and upon the real significance of the "presence and absence" hypothesis.

STRASBURGER has shown that females of *Lychnis dioica* attacked by *Ustilago violacea* become pseudo-hermaphrodites through the production of stamens, which however are non-functional, owing to the fact that the smut produces its spores in the anthers. This seems to justify his conclusion that each sex possesses some of the potentialities of the opposite sex.

The view is expressed that the sexes represent alternative states which in different species may be attained in various ways, through either quantitative or qualitative changes, additions, subtractions, substitutions, or transformations, and that in some instances the action of environment may prove effective in determining which of these states shall find expression. Nearly all the recent investigations indicate, however, that sex is at least predominantly dependent upon the genotypic nature of the individual.

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REPRODUCTION BY LAYERING AMONG CONIFERS

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WILLIAM S. COOPER

(WITH ONE FIGURE)

Many types of plants multiply more or less by layering, or may be made to do so by artificial means. The fact seems not to be well known that various conifers, particularly members of the genera *Picea* and *Abies*, possess this power and multiply by it to some extent. Having by accident discovered a case of layering in the balsam fir (*Abies balsamea* [L.] Mill.) during the course of ecological work on Isle Royale, Lake Superior, I found that the habit was a factor of considerable importance in the dynamics of the forest. Investigation into the literature of the subject brought to light a few scattered references to layering of coniferous trees, which are noted below. It is not probable that the list is exhaustive.

I. Literature

The earliest description that was found was contained in LOUDON'S *Arboretum et Fruticetum Britannicum* (8), vol. IV, pp. 2297–2298. The author quotes Mr. JAMES M'NAB in *The Gardener's Magazine* as follows:

> From the pendent habit of the lower branches of the spruce (*Picea excelsa* Link) some curious anomalies are occasionally found in its habit of growth. The shoots next the ground, when they have attained a considerable length, naturally rest on the soil at their extremities; and the soil being kept moist by the shade of the branches, these often root into it; and the points of their shoots taking a vertical direction, a series of new trees are formed in a circle round the old tree.

A particular specimen, growing in Scotland, is described thus:

> Many natural layers from the trunk and from the primary substems have taken root, so as to form a double series of young trees in two concentric circles round the parent trunk.

A little farther on is the following:

> That portion of the branch which is between the trunk of the original tree and the part where it roots into the ground, and which is sometimes several feet in length, rarely increases in diameter after its extremity has rooted. . . . .

The branches proceeding from the primary substems have also branches, equally healthy with themselves, proceeding from them, and with every appearance of their producing others. . . . . The primary substems, which constitute the inner concentric circle of young trees, vary from 8 feet to 25 feet in height; and the secondary substems, which form the trees of the outer circle, are from 4 feet to 10 feet high. There are upward of thirty rooted stems surrounding the mother tree, and 30 feet is the greatest diameter of the space covered by stoloniferous branches; though in one case a secondary layer has reached as far as 18 feet from the main trunk.

LOUDON also mentions cases of abundant layering in *Abies nigra* (*Picea mariana* [Mill.] BSP.).

KUNZE (**7**) also refers to M'NAB'S observations and concludes from these and other cases that "Coniferae, especially the Abietineae, possess widely extended power of root formation and are able to send out rooting shoots."

KIHLMAN (**6**) notes that *Picea excelsa* growing at the arctic tree line in Lapland spreads extensively by layering. He describes the occurrence of the habit as follows. The lowest branches often have roots, and from their tips new erect shoots develop, which become treelike in form and come to lead independent lives; from this results a complex of shoots and small trees of various ages, which is very sharply bounded, and which often arises from a single parent. Such a group, 4 meters in diameter, included 42 stems more than 4 cm. thick, besides numerous smaller ones. The age of such a centrifugally spreading group of spruces may almost be unlimited. He distinguishes two habit varieties of *Picea excelsa*. One possesses a tall cylindrical crown, often extending to the ground, the lower branches seldom rooting, and the life of the individual thus ending with the death of the main trunk. The other variety, characteristic of the region of the northern limit of the spruce, is low and scrubby, and layers abundantly as described above.

CHRIST (**2**) refers to layering in *Picea excelsa* as of rare occurrence, and names such forms *Picea excelsa forma stolonifera*.

GOEBEL (**5**) mentions cases of layering in *Picea excelsa*, *P. nigra*, and *Abies sibirica*.

SCHRÖTER (**11**) describes and illustrates something very similar in the case of *Pinus montana* in the timberline belt of the Alps.

He speaks of "horizontal snakelike branches crawling over the ground, ascending or erect at the ends," but does not state, nor do his figures show, that these branches take root.

According to MAYR (9) all deciduous trees and conifers are able to produce roots when branches or weak stems are bent down and placed in contact with the ground for a time. He mentions the following genera as among those that have been observed to reproduce by layering: *Abies, Picea, Pinus, Larix, Pseudotsuga, Chamaecyparis, Cryptomeria.*

MIGULA (10) briefly notes the habit, and gives an illustration of a spruce (*Picea excelsa*) surrounded by a circle of young trees developed from layered branches.

VOGTHERR (13) speaks of the habit as occurring frequently, though often overlooked, and states that it is commonest in moist habitats in northern latitudes and in mountain regions.

Reproduction by layering among conifers has been reported in America, so far as I have been able to discover, in two species only, both of the genus *Abies.*

SUDWORTH (12) in discussing the reproduction of the alpine fir (*Abies lasiocarpa* [Hook.] Nuttall) says (p. 111): "Occasionally at high elevations branches lying on ground take root (layer), from which, however, reproduction is probably rare."

In *Silvical Leaflet* (4) of the Forest Service, devoted to *Abies lasiocarpa*, is the following paragraph:

> Alpine fir frequently exhibits a tendency to reproduce by layering. The lower branches, which are procumbent, become covered with earth, roots are produced, and the branches increase in size and assume an upward curve. It is doubtful, however, if the tree ever actually reproduces itself in this manner. The tendency becomes more apparent with increasing altitude, the main trunk becoming shorter, while the layered branches form a saucer-like whorl at its base.

CLEMENTS (3), speaking of the same species in the Colorado mountains, states that "all the young firs examined had started by layering from the lower branches of parent trees."

Concerning the eastern balsam fir (*Abies balsamea* [L.] Mill.) I have found but one notice of the habit. CHITTENDEN (1) in discussing the timberline trees of the White Mountains says:

Balsam, at such elevations, rarely matures its seed, reproduction being dependent on seed blown up from below and on the layering of the trees themselves. Branches so layered are often found growing as independent trees, the connecting branch having decayed. The rooting always proceeds from dormant buds. Prostrate balsam occurs at an altitude of 5500 feet on the Presidential Range, where it reproduces almost entirely by layering. At an elevation of 4900 feet cones are borne sparingly, but even here reproduction by layering exists.

II. Layering as observed on Isle Royale, Lake Superior

Upon Isle Royale the layering habit manifests itself as follows. In the forest one frequently comes upon small groups of young balsams, often of about half a dozen individuals of various sizes. These upon superficial inspection would easily pass for a cluster of seedlings, but if the group be carefully dug up, all the young trees will be found to be connected with each other a little below the surface of the ground. The way in which the layering comes about was found to be as follows. The lower branches of the balsam droop more or less, and the middle portion of such a branch frequently becomes covered with moss, litter, and humus. If the point of origin of the branch is very close to the ground, the connection soon becomes entirely concealed; this seems to be the case more often than otherwise. The covered portion now produces roots abundantly, and the tip becomes erect, loses its dorsiventral character, takes on radial symmetry, and is to all appearances a perfect miniature tree.

Layering may take place at any stage in the life of the tree. Sometimes the layered branch may be only a few years younger than the parent and not very perceptibly smaller, showing that it must have developed from one of the very earliest branches. Mere seedlings were sometimes seen with layered branches about as large as the parent. The daughter trees often produce a second generation, and it is in this way that the groups of apparently independent saplings come into existence. On the other hand, cases were found where a mature tree was layering through branches that had their points of origin a number of decimeters above the ground. Several of the lower branches of a mature tree may layer, producing a circle of young trees around the parent, and numerous

cases were found in which the layered branches themselves had given rise to secondary groups, the connection with the original tree being still maintained.

There is abundant evidence that in many cases the layered branches become independent trees by the decay of the connecting portions. In fig. 1 it may be seen that the layered branch near its point of origin is extremely slender, while in the region where the roots have developed and in the subaerial portion it is thick. The transition from thin to thick is frequently very abrupt. This points toward the conclusion that the young tree is deriving by far the greater amount of its sustenance from its own root system, and that if the connection should be broken it would be entirely able to care for itself. The underground portion was often so weak that in spite of the greatest care it was severed in the process of uprooting. In many cases also the decumbent bases of independent young balsams indicate that they once had a horizontal connection with some neighboring tree (see *a* in fig. 1).

Some examples will make clear the various forms which the habit of layering takes.

1. A very typical case is seen in fig. 1. The oldest stem shown in the photograph is at *1* (all but the base has been removed for the sake of clearness). That this is itself a layered branch of a still older tree is indicated by the long rhizome-like structure (*a*) extending horizontally toward the left. The character of the well formed young tree *2* as a layered branch of *1* is evident. Branch *2* is one meter high. Branch *3* is connected with *2* by way of *c*, and has itself given rise to *4;* the latter finally has produced *5*. There are thus represented five generations of upright stems produced by repeated branching and layering. Each except the youngest possesses a well developed root system of its own, and in every case except the last the horizontal connecting stem behind the region of vigorous rooting has remained practically without further development. The constriction where *b* joins *1* is especially evident. Branch *5* receives all its nourishment from *4*, and the latter probably still derives much from *3*.

2. A balsam 2 meters high, which had died very recently at the age of 46 years, itself apparently a layered branch, had given rise

through a lower branch to a young tree 7.5 dm. high, 24 years old, 2.5 dm. distant from the parent. This daughter tree was found to have produced four smaller ones, 1.5–6 dm. in height, with ages ranging from 16 to 22 years.

3. That the habit may show itself even in large and mature individuals is proved by the following case. This tree, a balsam

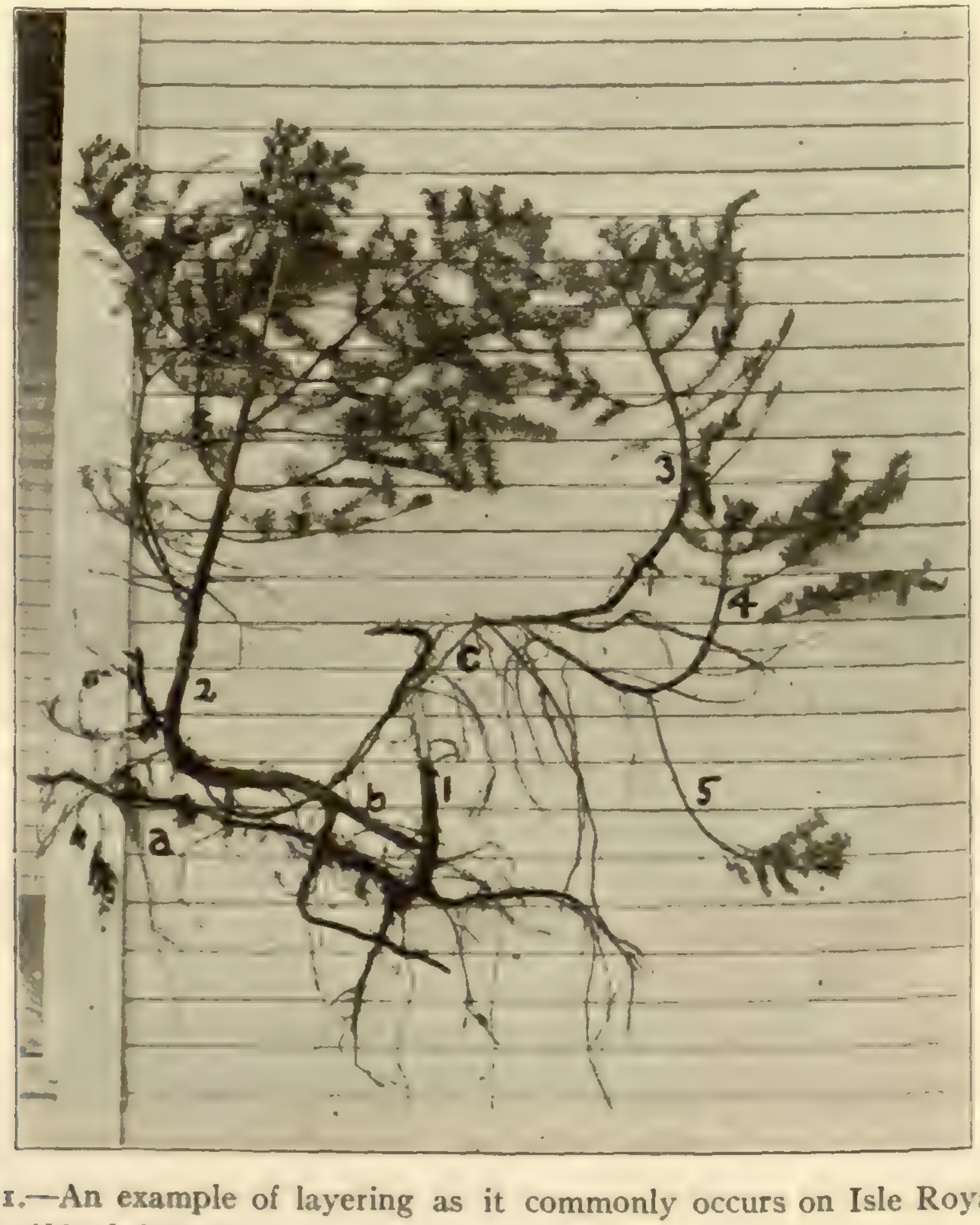

FIG. 1.—An example of layering as it commonly occurs on Isle Royale, Lake Superior; *Abies balsamea*.

1.5 dm. in diameter and 85 years old, had given rise to a daughter tree through a layered branch which started 7.5 dm. above the ground. The outer portion of this branch was soil covered and had well developed roots. At a distance of one meter from the parent it became a symmetrical tree 1.3 m. high. The same large branch had also produced two smaller trees by the layering of secondary branches.

4. A balsam growing in a large rock crevice at the forest edge on an exposed shore had several layered branches, erect at tip, through the soil at the general level of the ground. Several similar branches, at about the same elevation but in line with the crevice, descended into it somewhat, but their ends were erect, radially symmetrical, and perfectly treelike. Since the crevice was a foot wide and contained no soil, no roots were formed in this case, and these branches remained entirely dependent upon the tree.

Aside from the balsam, layering was less frequently observed in every one of the coniferous trees that occur upon Isle Royale. It was fairly common in the case of the black spruce, perhaps being favored by the pronounced droop of the lower branches of that species. The black spruce occurs sparingly in the upland forest, and in this habitat the layered branches were identical in behavior with those of the balsam. Black spruces and tamaracks growing in bogs were found to layer abundantly through the rapidly growing sphagnum. Specimens of white spruce were found upon nearly bare rocks, whose lowest branches, covered with a thin mantle of humus, had developed the layering habit to such an extent that the parent had become entirely surrounded by a group of daughter trees. Similar groups were seen in the case of arbor vitae growing in a river swamp.

III. Conclusions from data presented

From the material here presented we gather that the habit of natural layering among coniferous trees is common and widely distributed, though its importance appears to have been generally overlooked, at least in this country; that it is particularly characteristic of the closely related genera *Picea* and *Abies*, but is found in many other genera, among which are *Larix*, *Thuja*, *Pinus*, *Pseudotsuga*, *Chamaecyparis*, and *Cryptomeria;* that it is most prominent in northern and mountain regions, and that it occurs more frequently and attains more striking development with increasing latitude and altitude; that its best development is found at the extreme limit of the forest—the arctic tree line and the mountain timberline.

The general region of its occurrence is practically that of conifer

dominance; its increased development in high latitudes and altitudes is not so easily explained. VOGTHERR (13) correlates the layering tendency with a moist habitat, made possible by the low evaporation rate in northern and mountain forests, and it is doubtless true that moisture and absence of light are the factors that stimulate the buried portions of the branch to root production. But cases were noted (see example 4 above, and also SCHRÖTER 11), in which, although the end of the branch became erect and treelike, no portion was buried, and therefore no roots were formed. In other cases trees with layered branches were found growing in xerophytic situations upon the exposed rocky shores of Lake Superior. Timberline conditions, too, more often than not, are xerophytic in the extreme. The connection with a moist habitat thus seems not to be an essential one. In explanation of the striking cases of layering reported from the tree line in various regions (circles and double circles of daughter trees surrounding the parent), it may be noted that in such localities the forest is open, and the trees therefore, on account of abundance of light, are clothed with living branches to the ground. Moreover, they are as a rule short, bushy, and branchy, and the low crown tends to spread horizontally rather than to increase in height. Just such conditions as are found here (numerous healthy branches close to the ground) are those which would apparently most favor the appearance of the layering habit. In the endeavor to solve the problem, however, the meagerness of the data should be borne in mind. It may be that more extended and careful observation would prove that the habit is as common at low latitudes and altitudes as at high. Possibly the greater number of reports from arctic and alpine regions is due to the fact that the phenomenon is most easily observed there, or that individual cases of more striking appearance have been found. On Isle Royale, though the habit was exceedingly common, no such remarkable examples were discovered as those reported by LOUDON and KIHLMAN.

IV. Ecological importance of layering

The habit of layering, in regions where it occurs, must be included as an important factor in any investigation of forest

dynamics. For example, in the climax forest of Isle Royale there is an appearance of thick reproduction, with a great preponderance of balsam in the young growth. Upon superficial examination one would conclude that reproduction by seed is taking place at a tremendous rate. Careful investigation reveals that a large proportion of the apparent seedlings are in reality merely layered branches, some of them having originated from mature trees, and many others being groups of connected shoots which have started from a single true seedling. The same situation was found by CLEMENTS (3) in Colorado. It is evident that the effectiveness of this method of reproduction will have an important bearing upon the course of the succession in the forest. The habit is of special importance in the region of timberline, where, according to authors quoted above, it is sometimes almost the only method of reproduction.

V. Physiological bearing

There are also physiological problems involved in the phenomena of layering in this group of plants, which cannot at present be satisfactorily settled. These problems relate to the theories of orthotropism and plagiotropism and their mutual relations. The whole subject is at the theoretical stage, without adequate evidence in support of any of the various hypotheses. In the process of layering, the rooting (when it occurs) is simple enough as a response to moisture and absence of light. The change from dorsiventral to radial symmetry is to be expected as a result of the tip becoming erect, being an adjustment to changed light relations. The change in direction of growth from horizontal to erect is the part that is difficult to explain. It is bound up with the agencies which cause lateral shoots, ordinarily plagiotropic, to become orthotropic when the terminal shoot is removed or damaged. In the process of layering, it should be noted, this change takes place without antecedent removal of the main shoot. The case is thus somewhat different, but the same factors doubtless govern it. In the present state of knowledge relating to orthotropism, plagiotropism, and correlation, it will be useless to continue the discussion at length. One point however seems to be important enough in its bearing upon the

physiological side of the question to justify a few words in conclusion. GOEBEL (**5**, chapter iii), to explain the replacement of the terminal by a lateral shoot, offers the theory that the change in direction of growth of the lateral comes about because of changed conditions of nourishment. He thinks that the main transpiration current, which ordinarily goes to the terminal shoot where growth is most vigorous, is deflected when the terminal shoot is removed, and passes into the uppermost lateral. The great increase in nutrition acts as a stimulus, causing the lateral shoot to become erect. He describes several cases of layering among conifers, and attributes the change in direction of growth of the layered branch to the same factor. In this case the increased amount of food materials which acts as the stimulus is furnished through the agency of the newly formed root system. This theory would fit most of the cases of layering which have been described, but in one example which came under my observation on Isle Royale (no. 4 above) the change of direction of growth took place with absolutely no root formation. The same is probably true of those described by SCHRÖTER (**11**). Here are cases, therefore, where GOEBEL'S explanation certainly does not hold, and so far as this bit of evidence goes, it throws doubt upon his theory as a whole.

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THE ENDOSPERM OF ANGIOSPERMS

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 150

JOHN M. COULTER

In a recent analysis of all the available testimony in reference to the morphological nature of the endosperm of angiosperms, it seemed clear that certain conclusions might be reached, and the purpose of the present paper is to state them.

It has been assumed that the endosperm must be either gametophytic tissue or sporophytic tissue, and the arguments for each view are familiar. The perplexity has arisen chiefly from the feeling that gametophyte and sporophyte must be subject to rigid definition. When definitions become rigid, ideas become rigid also, and nature is always playing havoc with rigidity. If gametophytes and sporophytes are defined as x and $2x$ structures, respectively, straightway x sporophytes and $2x$ gametophytes are discovered. If sporophytes are defined as structures produced by fertilized eggs, the definition is contradicted by numerous sporophytes that are not the product of fertilization. In this way, every criterion suggested has found its contradiction. It is becoming evident that definitions must be elastic and not rigid, and that general situations rather than definite categories must determine conclusions. We have moved so far beyond the rigid categories of the days of metamorphosis, that it is surprising to find an equal rigidity in the days of alternation of generations.

Without citing an extensive and familiar literature, attention may be called to the various claims that have been made as to the morphological nature of the endosperm of angiosperms.

Ever since the comparative morphology of the vascular groups was uncovered by HOFMEISTER, belief has been general that the endosperm of angiosperms is gametophytic tissue which develops after fertilization. It was easy, even in the days of HOFMEISTER, and much more so now, to obtain from gymnosperms what seems to be abundant confirmation of this claim. Throughout that group there is a distinct tendency to differentiate eggs earlier and earlier

in the ontogeny of the gametophyte. When this differentiation occurs along with the first appearance of tissue after the free nuclear stage (as in *Torreya*), it is clear that the great bulk of endosperm tissue is developed after fertilization. When the differentiation occurs during the free nuclear stage (as in *Gnetum*), it is clear that all the endosperm tissue is developed after fertilization. It was very easy, therefore, to see in the endosperm of angiosperms only belated gametophytic tissue.

When the relation of the polar fusion to endosperm formation began to be appreciated, LE MONNIER (1887) suggested that this fusion is a sexual act, and that therefore the endosperm is sporophytic. This would mean that the embryo and endosperm are twin sporophytes, the latter for some reason not developing the organization of an embryo. This explanation of the polar fusion does not seem to have met with much approval. It is important to note, however, that lack of approval was probably due to the fact that there had developed already a considerable knowledge of the great freedom of nuclear fusions within the embryo sac and within the endosperm. Clearly all such fusions could not be sexual.

With the discovery of "double fertilization," the endosperm problem became conspicuous. One of the nuclei that enters into the triple fusion is plainly a male nucleus; one of the polar nuclei is sister to the egg nucleus, and this was taken to indicate its sexual character; the other polar nucleus has been regarded as vegetative in character. The fusion of an undoubted male cell and an assumed egg was regarded as an act of fertilization, and the product of such a fusion must be a sporophyte. This conclusion as to the nature of the endosperm is inevitable if the triple fusion is to be regarded as involving a sexual fusion.

If the endosperm is a sporophyte, it must be explained why it does not become organized as an embryo, but remains as formless tissue. Miss SARGANT (1900) offered a very ingenious explanation, effectively supported by what seemed to be confirmatory evidence. According to this explanation, the endosperm remains a formless mass of tissue (a "monster") because a vegetative nucleus enters into the fusion and interferes with the legitimate result. This view is attractive, but hardly explains the increasing number of

cases in which the so-called vegetative nucleus does not enter into the fusion, and still the product is only endosperm.

STRASBURGER analyzed the situation, and held to the original interpretation of the endosperm as gametophytic tissue, on the plea that there are two aspects of fertilization, one being fertilization as a stimulus to growth, the other being fertilization as a transmission of hereditary characters. These two aspects he designated respectively vegetative fertilization and generative fertilization. He saw in the result of the triple fusion only a stimulus to growth, resulting merely in tissue, and not a transmission of hereditary characters, which would express itself in an organization. Unfortunately for this view, all the phenomena of xenia are against it, for in such cases it is quite evident that characters of the pollen parent are transmitted to the endosperm by the male nucleus that enters into the triple fusion, but of course there is no sporophytic organization.

Furthermore, the cytological test for the two generations breaks down in this case, as it had in cases of apogamy and apospory, for the endosperm number of chromosomes, in case triple fusion has occurred, is neither x nor $2x$, but at least $3x$. To speak of $3x$ gametophytic tissue is to use some other test than the number of chromosomes. It must not be understood that this in any way affects the general contrast between gametophytes and sporophytes on the basis of chromosome numbers. A generation that follows a reduction division is of necessity an x generation; and one that follows fertilization is a $2x$ generation. But when the reduction division or fertilization does not occur, and still another generation follows, the chromosomes of that generation must become unusual in number, following an unusual situation.

It will be helpful to consider the cases of endosperm formation that do not involve triple fusion. This will enable us to recognize the fact that the origin of endosperm is not necessarily related to the triple fusion, and that we have in endosperm a constant product arising from variable antecedents. It is simple to put such cases into two categories: (1) multiple fusions, and (2) no triple fusion.

(1) The well-known case of *Peperomia* may represent the category of multiple fusions. In the fusion of 8–14 nuclei to form

the "primary endosperm nucleus," we observe an act too miscellaneous to represent anything so definite as fertilization. Moreover, we obtain positive evidence that in the embryo sac there is some condition that favors nuclear fusions, quite apart from what may be called sex attraction.

(2) Cases of no triple fusion, followed by endosperm formation, are numerous. In some instances, there is not even polar fusion, each polar nucleus initiating endosperm formation independently. In other cases, the male nucleus may fuse with either of the polar nuclei, the other nucleus remaining out of the combination, but the result is always the same. When the male nucleus pairs only with the micropylar polar nucleus, one might expect an embryo, if the latter nucleus is really an egg, but endosperm is the result. The increasing number of known angiosperms which are habitually parthenogenetic furnish cases of endosperm formation in the absence of the male nucleus. Of course in such cases the endosperm may be claimed to be parthenogenetic also.

The cases of so-called parthenogenesis among angiosperms illustrate a wider variation in the antecedents of endosperm formation than the mere absence of the male nucleus would seem to indicate. STRASBURGER has called attention to the fact that in the cytologically investigated cases of parthenogenesis there has been no reduction division, and that therefore the parthenogenetic egg is a $2x$ egg, just what it is after normal fertilization. If the failure of reduction results in a $2x$ egg, it must result also in $2x$ synergids, antipodals, and polars; in other words, the gametophyte has throughout the sporophyte number of chromosomes. And still, endosperm formation proceeds as before, when one would be justified in expecting embryo formation by sporophytic budding, a phenomenon very common in the tissues adjacent to the embryo sac. No one questions that the embryo is a sporophyte, whether it is a result of the act of fertilization or not, for it is recognized by its organization. It is pertinent to ask, therefore, why there should be any hesitation in recognizing the endosperm as gametophytic from its lack of organization, no matter how it originates. It is obvious that the constancy of endosperm lies in its structure and not in its origin.

From the facts in hand, the following statements seem to be justified:

(1) Endosperm formation is not dependent upon the presence of a male nucleus.

(2) Endosperm formation is not even dependent upon polar fusion.

(3) Therefore, both of these fusions may be regarded as *supplementary* rather than *determinative*.

(4) Endosperm formation does not even depend upon having been preceded by a reduction division.

(5) The fusions associated with endosperm formation do not represent a definite process, but are miscellaneous in number and order.

(6) The product of such fusions as do occur is merely an undifferentiated tissue, which practically continues the tissue of the gametophyte; that is, it is simply *growth* and not *organization*.

Conclusions

It seems evident that the egg has an organization peculiar to itself. A male cell may fuse with any other cell in the sac, and the result is only endosperm; but occasionally such a fusion (as with a synergid or a polar) results in an embryo. This implies that, for some reason, these ordinarily sterile cells have achieved the organization of eggs. It is this possibility that makes them *potential* eggs; but in the ordinary embryo sac of angiosperms there is only one *actual* egg, which means only one cell capable of being fertilized in any real sense, and therefore capable of producing an embryo.

Conditions in the embryo sac favor fusions of any free nuclei, in any number and of any origin. A male nucleus, perhaps, is more apt to enter into fusions than any other kind.

A male nucleus entering into a fusion may or may not express itself as a carrier of hereditary characters. If it does express itself in this way, it is like injecting certain gamete tendencies into a vegetative fusion; therefore, it is more probable that the male nucleus modifies somewhat the normal product than that the antipodal polar (a vegetative nucleus) modifies a normal product. In

other words, the vegetative fusion is more apt to represent the normal situation than a sexual fusion.

There is no necessary phylogeny of such a performance. It is more a physiological problem to discover the conditions in the embryo sac of angiosperms that favor miscellaneous nuclear fusions.

The final conclusion seems to be that free nuclei within the embryo sac, containing a variable number of chromosomes and reacting to one another in various ways, are in a condition to continue division, and this division is usually carried forward to tissue formation. The whole history of the megaspore and its products justifies us in regarding this tissue, however formed, as gametophytic.

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NOTE.—Since this paper was in type, there has appeared a paper by CAMPBELL on the embryo sac of *Pandanus*,[1] which supplies another illustration of the indefiniteness of the nuclear fusions within the sac. In this case there is an extraordinary development of antipodal tissue before fertilization, and a varying number of free antipodal nuclei fuse with the micropylar polar to form the large primary endosperm nucleus. In some cases two primary endosperm nuclei may be formed by these multiple fusions, and it would seem to make no difference in the result whether the "second male nucleus" fuses with one of them or with neither of them. In either event, it is obviously a vegetative fusion.

[1] Ann. Botany **25**:773–789. *pls. 59, 60. figs. 2.* 1911.

SOME PROBLEMS IN CECIDOLOGY

MEL T. COOK

It is very doubtful if any phase of biology has been neglected more than that very conspicuous and extremely puzzling branch known as cecidology. This subject in its broadest sense includes all forms of abnormal plant growth regardless of cause. It must include, therefore, not only the hypertrophies, but also the witches brooms. It must include the abnormal growths caused by flowering plants, fungi, bacteria, insects, nematodes, and chemical and mechanical injuries. It must also include that great number of abnormal growths from unexplained causes which are included under the general term of teratology. Unfortunately, many of the botanists have interpreted the subject to include only those cecidia which are the result of insect injuries, and have attempted to relegate the entire subject to the entomologists, although they have not hesitated to study the cecidia caused by nematodes and bacteria, which might just as reasonably be forced upon the zoologist and bacteriologist.

The fact that the mycologists have usually been interested in the fungi and not in the host plant, explains why so much interesting material has been thrown aside with the single comment, "bugs." But with the development of plant pathology, a branch of botany which is necessarily interested in the pathological condition of the host, there is no longer any excuse for not giving a reasonable consideration to all phases of cecidology.

It is the purpose of this paper to call attention to some of the problems involved in cecidology, and to their bearing on other phases of biology, more especially botany. Cecidology is as old as the science of biology, and cecidia are referred to in some of the earliest biological literature. That cecidia were the subject of speculation, if not of study, is evidenced in the writings of REDI,[1] who, like other vitalists of his period, believed plants were endowed with souls and that the soul of the plant controlled the formation

[1] REDI was born in 1626.

of both the egg (i.e., the gall) and the insect which emerged from it, and determined their specific characters. As in all other biological subjects, the first real scientific work was taxonomic in character, and in 1686 MALPIGHI, who was a physician to Innocent XII and professor of medicine in Bologna and later in Messina, published his *De Gallis*, in which he gave quite accurate descriptions of the known galls of Italy and Sicily. Following this work, which may be looked upon as the starting point for cecidology, LINNAEUS and many other later writers gave more or less attention to this subject, which has attracted so much attention in Europe during recent years. In America, the pioneers in this subject were Baron C. R. OSTEN-SACKEN, BASSETT, WALSH, RILEY, FITCH, SHIMER, and HARRIS, all of whom were entomologists.

Although the entomologists have done more work in cecidology in both Europe and America than the botanists, their work has been no broader. The entomologists have studied the insects and described the cecidia which were attributed to them, and in the case of the injurious species have devised means for their control. The botanists have done the same work for fungi which cause cecidia, and have also invaded the fields of the bacteriologist and zoologist and studied not only the cecidia produced by bacteria and nematodes, but have even studied the organisms.

Taxonomy seems to be the forerunner of all lines of biological work, and this has been true of cecidology, but we have now reached a point from which we can extend our studies into other phases of the subject. We can now study the subject with reference to other phases of biology, in fact other phases of biology are encroaching upon the subject of cecidology. With this new development, the entomologist, the mycologist, and others will continue to find ample fields for the study of taxonomy. The entomologist will also have those almost untouched fields of life history and of alternation of generations which came so near to demonstration by our fellow-countrymen, H. F. BASSETT, and which was afterward demonstrated by HERMAN ADLER.

The various groups of botanists will find especially rich and almost untouched fields in many directions. The anatomical and histological characters and the development of cecidia have

been the subject of extensive studies in Europe, but have received very little attention in America. These studies when properly carried out and correlated with the work of the taxonomists will in turn open broad and unexplained fields in evolution. The pathology of the plants which are suffering from the attacks of these many cecidia-producing organisms cannot be overlooked by the plant pathologists, who have no more right to refer insect cecidia to the entomologist than the surgeon has to send the patient suffering from a gun-shot wound to the gunsmith. Both the economic entomologist and the plant pathologist will find enough problems to keep them busy for many years to come. It is doubtful if the entomologist has said the last word on the *Phylloxera vastatrix*, *Schizoneura lanigera*, *Eriophyes pyri*, and many other cecidia-producing insects which attack economic plants; and it is undoubtedly true that the plant pathologist has scarcely touched many of the economic problems involving cecidia-producing fungi and bacteria. The cytologist will also find a field for his labor.

However, the most difficult and probably the most fruitful field is open to the plant physiologist; the character of the stimuli which excite malformation is a question well worth the attention of any group of scientists, and one which if answered may be very far reaching in its influence. The botanists have doped the plant with many chemicals, with some of which it may never come in contact in a state of nature; they have subjected it to the various kinds and degrees of gases, light, moisture, and temperature; treated it with electricity; prodded it with everything imaginable from a most delicate needle to a crowbar; and otherwise subjected it to various normal and abnormal conditions, but have made little or no effort to determine the character of the stimuli which cause the formation of cecidia. DARWIN and all his predecessors believed that the cecidia are directly or indirectly the result of a chemical secreted by the mother insect at time of oviposition; MALPIGHI believed that the chemical causes a fermentation of the juices; REAUMUR[2] held the same view, but also believed that the thermal effect of the egg and the character of the wound, which varies with the different species of the insect, are important factors. Sir

[2] Mémoires pour séries à l'histoire des insectes. Mémoire XII. Vol. III. 1738.

JAMES PAGET, as late as 1880, said that "the most reasonable, if not the only reasonable theory, is that each insect infects or inoculates the leaf or other structure of the chosen plant with a poison peculiar to itself." Unfortunately, this view is still held by most of our biologists, although the researches of the past thirty years have demonstrated that it is almost without foundation.

In 1881 Dr. HERMAN ADLER[3] published the results of his long and careful studies, in which he gave the first real scientific evidence concerning the nature of the stimuli and character of gall formation. According to his results, the fluid secreted by the oak-gall fly is not irritating, and is not a factor in gall formation, but may serve as an antiseptic dressing for the wound in the plant. This view is strengthened by BEYERINCK,[4] who demonstrated that the fluid is without taste or smell and not irritating when injected under the skin. ADLER advanced the idea, which has been affirmed by other workers, that in the oak-gall flies, whatever irritating chemical exists comes from the larva and not from the parent insect. ADLER also reports his observation on *Nematus Vallismierii*, one of the saw flies, which attacks the *Salix amygdalina*. In this case the female pours out an abundant glandular secretion at time of oviposition, and the gall is well formed before the larva emerges from the egg.

It is also well known that mechanical stimuli will frequently cause abnormal growths. However, accurate data upon the results of various stimuli is not to be found in our literature.

ADLER says that the cecidia always originate from the formative cells of the plant, and that if the stimulation is applied to any other than the formative cells, cecidia are not produced. This statement opens up an enormous line of work. While some scale insects cause hypertrophies, others do not. Who has traced the ramifications of the mouth parts of these insects through the tissues of the host? Why do some Uredineae cause cecidia while other closely related species do not? Who has traced the mycelia of these related species

[3] Ueber den Generationswechsel der Eichengallen. Zeitschr. Wiss. Zool. **35**: 151–246. 1881. Translated in 1894 by CHARLES R. STRATON.

[4] Beobachtungen über die ersten Entwicklungsphasen einiger Cynipidengallen. Naturk. Verli. der Kon. Akad. Deel **22**:179. 1882.

in their ramifications through the tissues of the host plants? Who has solved the chemical and enzyme relationships which may exist between these fungi and their hosts? If the insect cecidia are the result of chemical stimuli, how about the myco-cecidia? If the insect cecidia are due to mechanical irritation, how about the myco-cecidia? If the insect cecidia are the result of irritation applied to the formative cells, is the same thing true for the myco-cecidia? By what school of biologists should these problems be worked? Will not the solution of one set help in the solution of others?

The writer is not presenting these questions for the purpose of controversy, but merely to call attention of students to this enormous field of plant pathology and plant physiology. Give us more data concerning the relationship between parasite and host plant, regardless of the character of the parasitic organism. Let us tear away the artificial barriers and give the broadest study to these problems.

DELAWARE AGRICULTURAL EXPERIMENT STATION
NEWARK, DELAWARE

AN ELECTRICAL CONSTANT TEMPERATURE APPARATUS

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 151

W. J. G. Land

(WITH FOUR FIGURES)

The temperature of incubators heated with gas taken directly from the mains is very irregular when an attempt is made to control the flow with mercury-actuated thermostats commonly used. Most mercurial thermostats will compensate for slight variations from the mean gas pressure, but not for large ones. The rise in temperature in the water-jacketed incubators used in the Hull Botanical Laboratory for paraffin infiltration was so sudden and so high that delicate plant tissues were often much distorted.

Electrically controlled heaters have been placed on the market recently by makers of repute, but the price of the apparatus ($50 and $100) is unreasonably out of proportion to the cost of material and labor.

In order to test the effect of definite temperatures on plant tissues for a longer time than is usually employed in imbedding, and having a direct current of 110 volts constantly on in the laboratory, the problem of devising a simple and efficient electrically controlled heater was first attacked about four years ago. The conditions of the problem were that the apparatus must maintain a definite temperature constant within very narrow limits for weeks at a time, must be easily adjustable to temperatures ranging from 40° C. to 80° C. with certainty, must be absolutely automatic in action, must be readily attachable to the usual type of ovens, must require practically no attention to keep in order, must be simple and inexpensive to construct, must use a minimum quantity of electricity, and must not be easily put out of adjustment by inexperienced or meddlesome persons.

For over two years the apparatus here described has replaced the gas heaters in this laboratory, with satisfactory results. The risk of fire, always great when gas is used, has been eliminated.

So many requests for information concerning the apparatus have been received that it has become impossible to give individual replies.

The apparatus consists of a metallic thermostat (fig. 1) placed on a shelf in the oven, a water-jacketed heating coil (fig. 2) fastened to the bottom of the oven in such a way that the water jacket of the coil forms a continuous system with that of the oven, and an automatic switch (fig. 3) placed wherever convenient.

The thermostat (fig. 1, *n*) is a thin strip of iron about 1 mm. thick and 2 cm. wide, firmly riveted to a strip of zinc the same width and

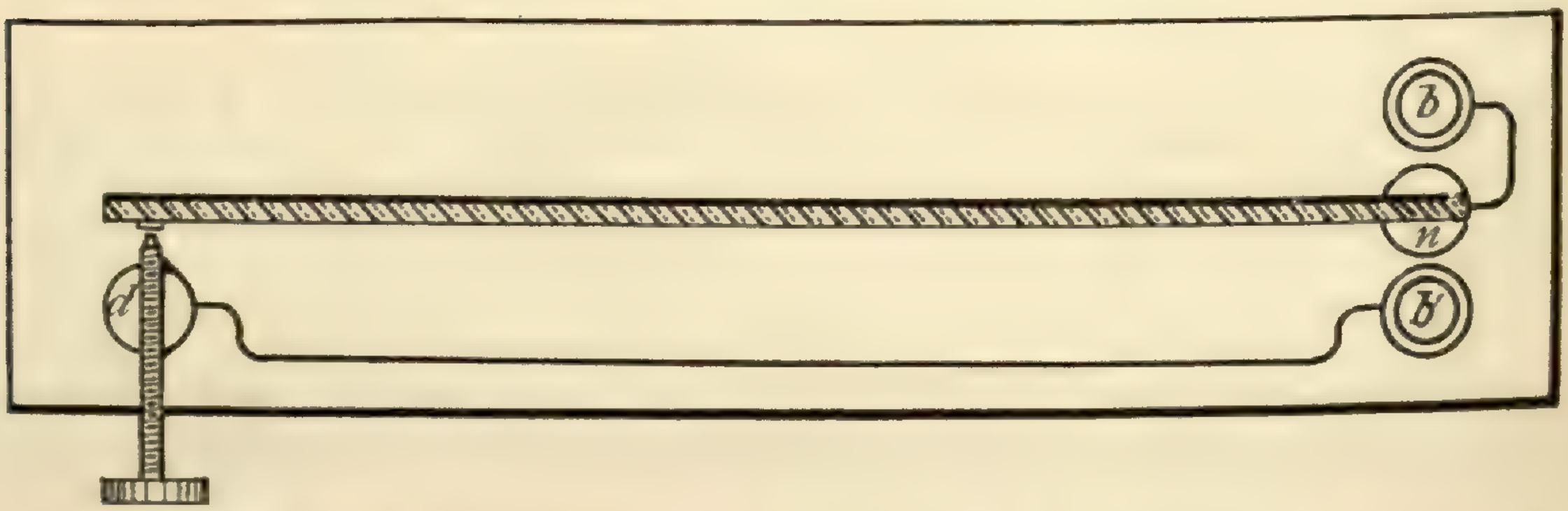

FIG. 1.—Diagram of thermostat and connections; *n*, thermostat of zinc and iron; *d*, screw for adjusting temperature; *b*, *b'*, binding posts to connect with *t*, *t'* of the switchboard.

from 1.5 mm. to 3 mm. thick. One end is fastened to a brass post set rigidly on the slate base, and the other end swings free. The free end of the metal tongue has a contact point of platinum fastened to the zinc side near the end. The adjustment for temperature is made with a platinum-tipped screw (*d*) set so that its point can always be brought in contact with the platinum disk on the metal tongue. The metal tongue and the adjusting screw are connected respectively with the binding posts (*b*, *b'*), as shown in the diagram.

The base of the thermostat should be made long enough to fit easily in the oven, the ends resting on ledges provided for the upper shelf. The sensitiveness of the thermostat depends, of course, on the length of the metal tongue. If extreme sensitiveness is required, it may be made nearly twice the length of the base and bent to a U, or it may be much longer and coiled. In practice 20 cm. has been found satisfactory. The zinc strip should not be thinner than

1.5 mm., or the thermostat will respond unpleasantly to any tremor of the bath or even in the laboratory building. If desired, brass or aluminium may be substituted for the zinc. The regulating screw should be made long enough to provide for quite a range of temperature. When the thermostat has been adjusted to the required temperature, it will need no further attention, except perhaps to brush the dust from the contact points at very long intervals. To raise the temperature turn the screw to the right, to lower it turn it to the left.

The heater (fig. 2) is a water-jacketed resistance coil of brass tubing and German-silver resistance wire. The tubing need not be thicker than 1 mm. The coil should be proportioned to the size of the oven it is intended to heat. For ovens having internal dimensions of 20×25×26.25 cm., and for temperatures of 30°–80°C., the size given here has been found suitable. Such a coil, however, will heat much larger ovens satisfactorily. The brass tubes should be about 15 cm. long. The resistance coil is four layers of no. 21 German-silver wire, wound on a tube 3 cm. *inside* diameter. The layers of wire are carefully insulated from the tube and from each other with asbestos paper about 0.6 mm. thick. The wire is wound with an engine lathe 24 turns to the inch under considerable tension, and the ends are brought out to binding posts (s, s') in the slate head of the coil. Wound as described, the current at 110 volts measures about 2.2 amperes.

The water jacket is made of 3 concentric brass tubes, the outer one being 6.25 cm. in diameter, the middle one 4.5 cm., and the inner one 3 cm. *outside* diameter, so that the tube of the heating coil will slip over it in close contact. The inner tube is closed at the lower end with a brass disk soldered tightly in place. The upper end remains open, and is fastened to the middle tube by a brass ring. The lower end of the middle tube is in turn fastened in a similar manner to the bottom of the outer tube. A hole is cut in the outer wall of the bottom of the oven, and the outer tube soldered directly to the bottom. If preferred, the outside tube may be threaded and screwed into a flange soldered to the bottom of the oven. If this method is used, a rubber gasket should be placed between the flanges, as shown in fig. 2. This arrangement

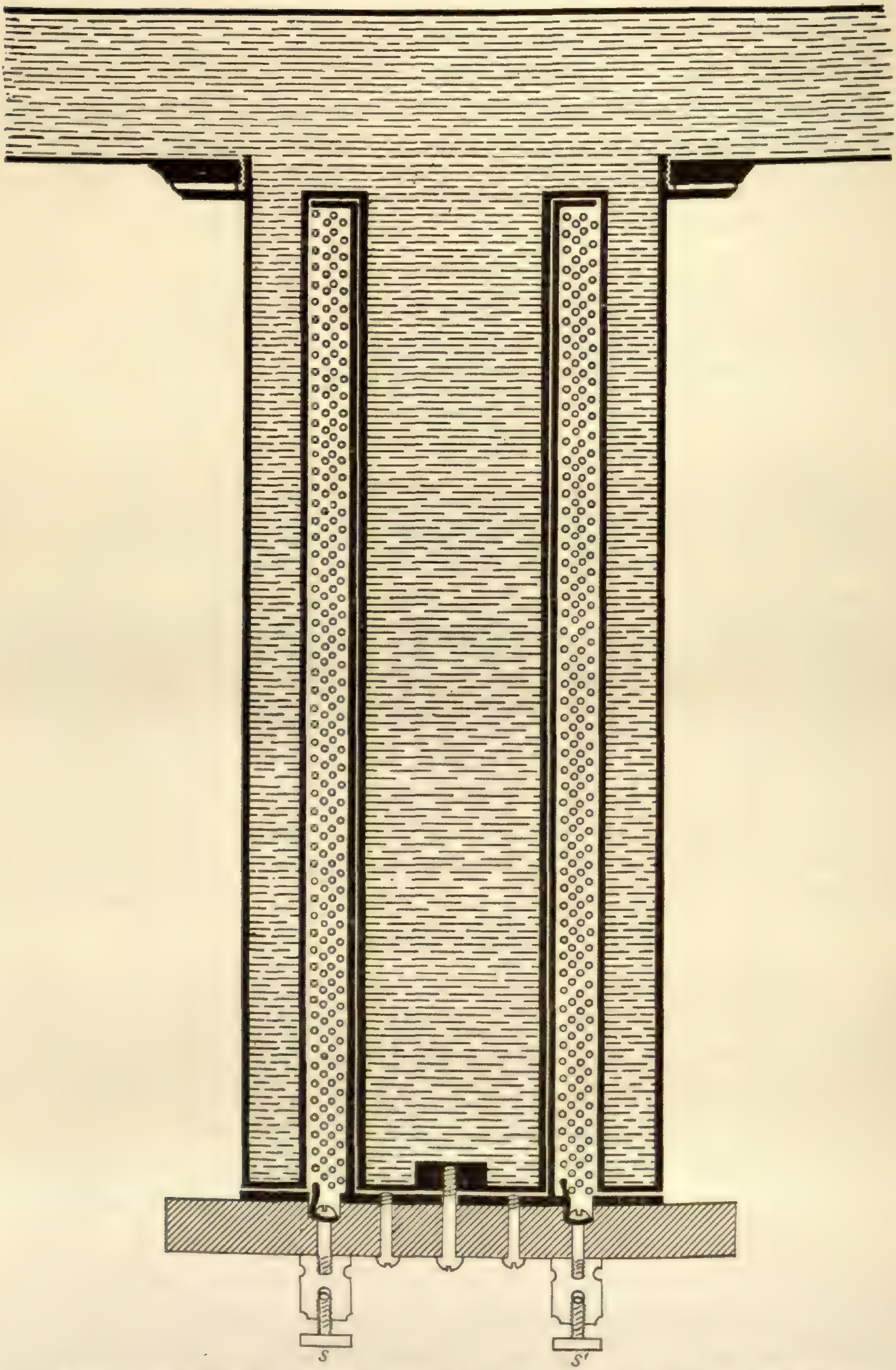

FIG. 2.—Median longitudinal section of heater, showing method of construction of water jacket and resistance coil, and how it is attached to the oven; s, s', binding posts to be connected with h, h' of the switchboard.

adds slightly to the cost, but will permit the sediment which appears in water-jacketed baths to be removed easily. Great care must be taken to have all joints absolutely water tight, since a leak will cause the destruction of the resistance wire in a few hours.

An inspection of the diagram (fig. 2) shows the arrangement is such that the resistance coil is completely surrounded by water except at the lower end, thus insuring rapid conduction of heat. Also the coil can be removed easily if repairs are ever necessary.

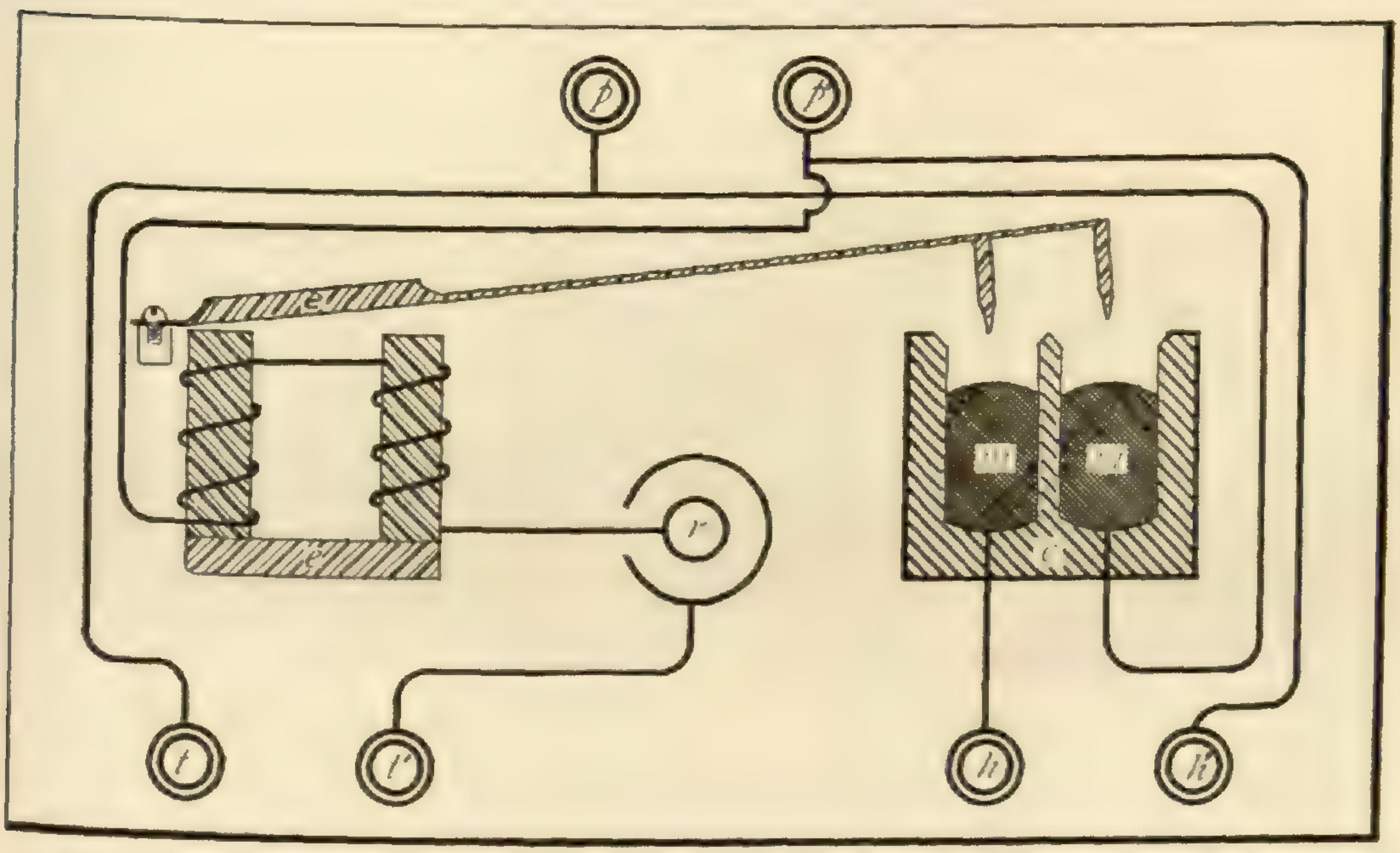

FIG. 3.—Diagram of automatic switch; p, p', binding posts to connect with source of electrical supply; e, electromagnet; a, armature and switch; r, gasket for lamp rheostat; t, t', binding posts to be connected with thermostat; c, container for mercury (m, m); h, h', binding posts to be connected with heating coil.

In two years' use, only one has needed repairs, made necessary by spilling water on the head of the coil when the water jacket was being refilled.

The automatic switch (fig. 3) is a slate base having an electromagnet (e), armature (a) with switch, and a lamp rheostat (r) at one end, and the slate cups (c) filled with mercury at the other. A convenient size for the slate base is 20×11.25 cm. The magnets, which can be had very cheaply from electrical supply houses, should have a resistance of about 20 ohms. The armature (a) should be fastened by a spring to a pillar rigidly attached to the baseboard,

and should extend about 15 cm. to form the arm of the switch. Care must be taken not to have the spring too strong, or the armature will not be pulled down when the current flows through the coils of the magnet. The spring may be much weaker if an 8 or 4 candle power lamp is used instead of a 16 candle power lamp rheostat. One wire connects the post p directly to t; the other post p' is connected through the electromagnet e and the lamp rheostat socket r with t'.

The switch end of the armature should have two iron pins extending downward at a right angle, sharpened, and tinned to insure good contact with the mercury in the cups c. In practice it is advisable to drill two holes in the switch arm, tap them, and use iron machine screws for contact points. The screws should be provided with lock-nuts to hold them at the proper length. Switch points gradually wear away, due to the small arc which always occurs when contact with the mercury is broken. The machine screw device permits compensation for this wear. The screws should be sharpened of course, to minimize splashing, and tinned.

The double cup (c) for holding the mercury (m, m) should be made of slate. A convenient sized block is $5 \times 3.75 \times 2.5$ cm. The holes for mercury should have a diameter not less than 1.25 cm., preferably 2 cm., and the edges should be chamfered. The mercury oxidizes somewhat rapidly, and in consequence the volume should be rather large. Oxidation of the mercury is the chief defect of the apparatus, but no way has yet been found to prevent it. To compensate for oxidation, a small quantity of mercury must be added occasionally. One wire connects the post p with one of the mercury cups, the other cup is connected with h. The post p' is connected directly to h'.

The switch (fig. 3) may be put in any convenient place, preferably out of reach of inquisitive persons. Attach the heating coil (fig. 2) to the oven and place the thermostat (fig. 1) inside the oven on the upper ledges and connect the posts p, p' of the switch with any convenient lamp socket, fill the cups c with mercury, screw a lamp in the socket r, connect the posts t, t' with b, b' of the thermostat. Connect h, h' (fig. 3) with s, s' (fig. 2) of the heating coil. These connections are shown in fig. 4, a photograph of the apparatus.

It is realized that most botanists are not electricians, and therefore the description of the construction and wiring of the instrument is not written for experts.

The action of the apparatus is as follows: When the platinum points of the thermostat are in contact, the current flows through

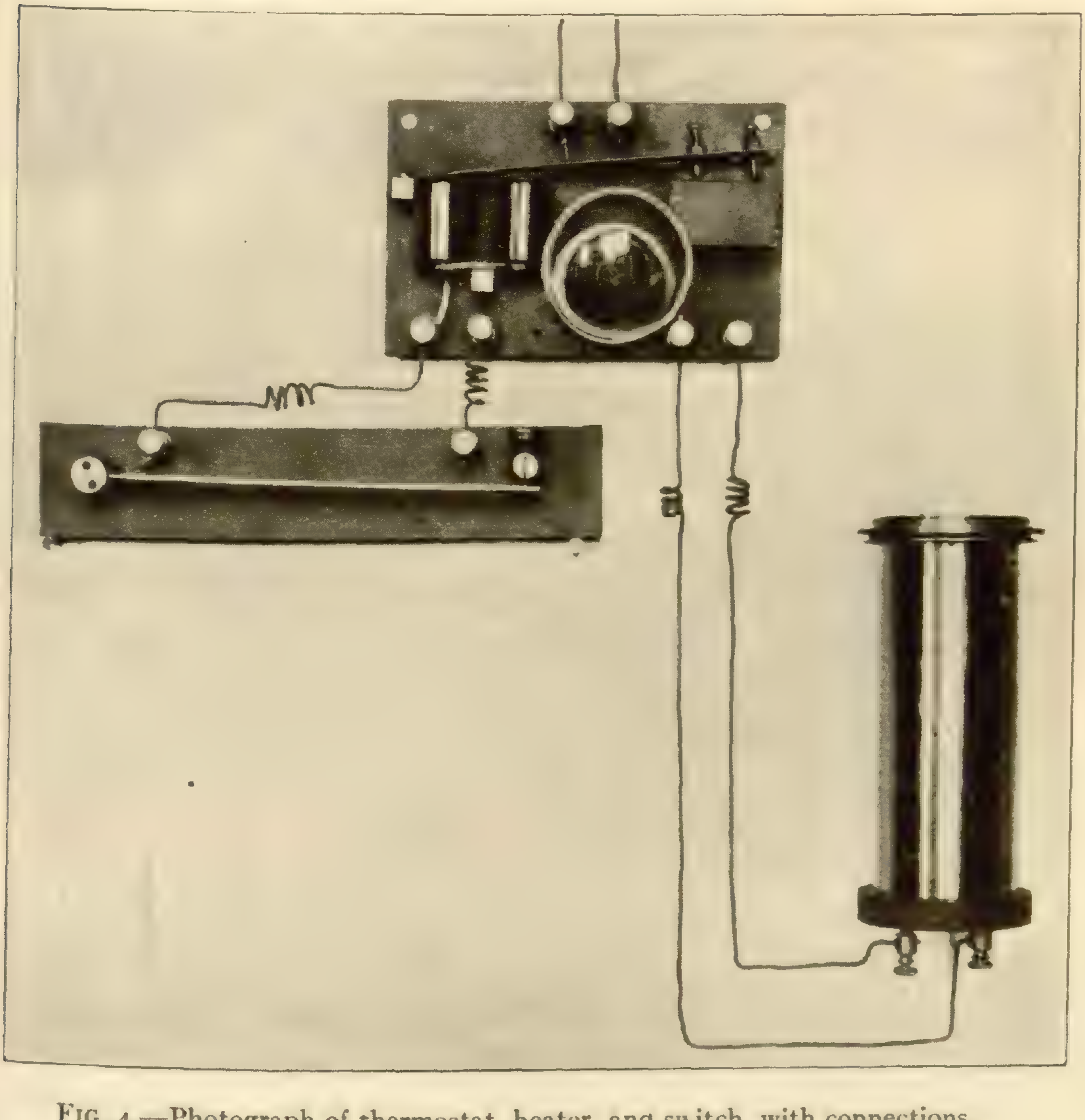

FIG. 4.—Photograph of thermostat, heater, and switch, with connections.

the electromagnet, the armature is drawn down, closing the switch and making a circuit through the heating coil. The circuit will remain closed only so long as the platinum points of the thermostat are in contact. As the temperature of the oven rises, the platinum points are separated, the circuit through the electromagnet is broken, and the switch is opened by the release of the armature.

When the temperature of the oven falls below the required point, the thermostat again functions and the switch is instantly closed. This action continues automatically as long as the current is supplied, or until the mercury in the cups is all oxidized. In one instrument it was found that a difference of 0.01° was sufficient to actuate the mechanism. As has been said before, turning the adjusting screw to the right adjusts for higher temperatures, and vice versa. It will be seen that the two circuits are absolutely independent of each other, and that when the oven is at the required temperature both circuits are broken; that the electricity is only on when the temperature is below the required point.

Because the switch closes so sharply when the thermostat functions, it is advisable to drill a small hole in the core of the magnet nearest the switch and insert a rubber plug for a buffer. If the mercury splashes too much, rubber corks, with a hole in the center, may be put in the tops of the cups. The flash which occurs when the switch points leave the mercury is bright, but it does no harm.

It is possible to use an alternating current, but it is very difficult to adjust the armature spring so as to avoid the unpleasant humming. It is planned to try a weighted or balanced armature with alternating currents. A battery may be used to actuate the switch if magnets of lower resistance are used, and the lamp rheostat replaced with a plug; then the alternating current may be used to heat the coil in the oven.

If preferred, the lamp used for a rheostat may be placed in the oven and connected to the socket on the switchboard with a cord and plug. This arrangement is very convenient, for the instant the door of the oven is opened the lamp is lighted. Also the heat of the lamp increases the efficiency of the apparatus.

Anyone at all familiar with tools can construct the apparatus at a cost of about $3.75 for material. Of course he must have access to an engine lathe to wind the coil so that the wires will not touch each other. After the first experimental instrument was found to work satisfactorily, the interest of a very expert mechanician, Mr. A. W. STRICKLER, 1311 E. 57th St., Chicago, Ill., was enlisted. He suggested many improvements, always having in mind increase of efficiency and lowering of cost. It is largely due

to his interest in the problem and his skill in construction that the apparatus has proved so efficient in this laboratory. He has recently devised a form of this thermostat which can be used with safety where explosive gases are present. He finds that when made as described here the cost should not exceed $15.00 for the apparatus complete and ready to attach to the incubator.

THE UNIVERSITY OF CHICAGO

BRIEFER ARTICLES

APOGAMY IN *PELLAEA ATROPURPUREA*

In the course of a study of fertilization and related phenomena in several ferns, a culture of *Pellaea atropurpurea* (L.) Link was found to have developed embryo sporophytes apogamously. The spores of this species were collected in October and sown on clay soil December 13, 1910. The soil was sifted into a small pot, moistened with water, and sterilized in an oven. The culture was kept under a bell jar in a Wardian case in the university greenhouse. Watering was found necessary but once, and was accomplished from below with distilled water.

The prothallia grew rather rapidly, and hundreds carefully examined at various times showed no indications of antheridia or archegonia. Two and one-half months after the spores were sown, the first indications were noticed of the development of apogamous embryos. Many prothallia were again examined on both surfaces for the appearance of sex organs, with negative results. On March 13, 1911, 110 prothallia were examined with special care; 47 bore sporophytes in various stages of development, but no sex organs were found in any case.

At an early stage in development it is difficult to distinguish between young antheridia and rhizoids. Young antheridia may be hidden among the rhizoids and escape attention; rhizoids, however, were in no case produced in great abundance in the culture in question. Thus the possibility is not excluded that rudimentary antheridia may have been formed; but my observations make it certain that none developed beyond the earliest stages, and that no archegonia were produced on these prothallia at any time.

The prothallia of this fern are of a darker green color than the prothallia of several other species in my cultures. They are generally heartshaped with a deeply cut notch, but many irregularly shaped prothallia occur. The first appearance of the apogamous embryo is indicated by a small darkened area usually a short distance back of the growing point. This, as sections made at this time show, represents a region of active division, the prothallial cells concerned being much

smaller than the neighboring ones which are not concerned in embryo formation. Embryos are formed on the inner sides of the lobes, as well as a short distance back of the apical notch. Long ribbon-shaped prothallia without apical notches also develop sporophytes at their distal ends. Sporophytes are often formed, therefore, in regions quite distinct from the meristematic area in which archegonia are ordinarily developed.

Soon after the beginning of embryo development, hairs appear surrounding the region of active growth. These originate from the area of the prothallium which is involved in the development of the embryo. Still later, the embryo projects from the prothallium, somewhat inclosed by the hairs, each of which is composed of several cells with large nuclei. As the embryo continues to grow, the primary leaf, from the petiole of which numerous hairs develop, makes its appearance. Later the primary root and stem are formed. At no time was there any evidence of the development of a structure which could be thought to correspond to a foot. In several cases two sporophytes began their development on the same prothallium. From studies so far made, it appears that both interior and surface cells of the prothallium are involved in the formation of the sporophyte.

During the present season, apogamous embryos have begun their development upon a large number of prothallia of this species in four cultures growing upon peaty soil. The first embryos were observed about one month after the sowing of the spores.

So far as I know, apogamy has not been previously reported in *Pellaea atropurpurea*, although WORONIN (1907) reported its occurrence in *P. flavens*, *P. nivens*, and *P. tenera*.—W. N. STEIL, *University of Wisconsin, Madison.*

CURRENT LITERATURE

BOOK REVIEWS

Vegetation der Erde

IX. Africa

As previously noted in these pages,[1] Engler has in contemplation an elaborate phytogeographic treatment of tropical Africa. The second volume of this series was the first to appear, and it is now followed by the first volume, which is issued in two parts.[2] The first volume is devoted to as much detail as is now possible to a consideration of the vegetational conditions of Africa. This volume makes it particularly clear that Africa is no longer the "unknown continent"; particularly is this true, so far as tropical Africa is concerned, of the German possessions, each of these being well delineated phytogeographically by maps in colors. Most of the volume is taken up by a presentation of the chief phytogeographical subdivisions of Africa, which, as here treated, are (1) Mediterranean Africa with the bordering parts of the Sahara, (2) tropical East Africa, (3) the southwestern region of winter rain, (4) the summer rain region of West Africa, (5) Macronesia. This portion of the work is richly and beautifully illustrated by photographs of desert landscapes in North Africa, cuts of representative Saharan plants, and by similar photographs and cuts in much greater number from tropical East Africa, including especially Abyssinia, the Somali Peninsula, and German East Africa. The account of the summer rain region of West Africa also is very full and is finely illustrated, especially in the portions dealing with the German territory. The work closes with a treatment of the general geographic conditions (including temperature and precipitation data, and an account of the various types of soils), a short description of the regions at different altitudes, a brief survey of the plant formations, and an account of the floral constituents and the general floristic relationships of Africa. Under the last head many genera are tabulated as to their affinities, whether pantropic, paleotropic, endemic, etc. Also there is a short account of the geological development of the present vegetation.

XI. The Balkan countries

Adamović, who for many years has published important papers dealing with the vegetation of Servia and neighboring lands, has now issued a mono-

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[1] Bot. Gaz. **50**:468. 1910.

[2] Engler, A., und Drude, O., Die Vegetation der Erde. IX. Engler, A., Die Pflanzenwelt Afrikas insbesondere seiner tropischen Gebiete. Bd. I. pp. xxviii+1029. *maps 5. pls. 47. figs. 708.* Leipzig: Wilhelm Engelmann. 1910. *M* 60 (subscription *M* 45).

graph of the Balkan countries for the *Vegetation der Erde*.[3] After an account of the topography, hydrography, geology, and climate, there is a rather detailed treatment of the ecological factors, considerable attention being paid to the soil and to the plants which are confined to or are dominant on certain soils. Approximately half of the work is devoted to a consideration of the plant formations. Among the more interesting of these are such Mediterranean formations as (1) the mixed forests with the manna ash (*Fraxinus Ornus*); (2) the *Aesculus* forests; (3) the Sibljak formation, which is a type of thicket characteristic of the Balkan countries, including *Paliurus*, *Cotinus*, *Syringa*, and other representative forms; and (4) the Tomillares, a xerophytic formation, dominated by coarse herbs. On the hills and mountains there occur formations comparable to those of Central Europe, such as oak and chestnut forests, forests of *Pinus leucodermis* and *P. nigra*, fir forests, forest of *Picea Omorica*, beech forests, sand formations, mountain meadows, and mountain thickets. The third and fourth parts of the volume are devoted respectively to an account of the floristic composition and relationship of the region both horizontally and vertically, and to a developmental treatment of the Balkan vegetation from the Tertiary to the present. The region contains many interesting Tertiary relicts. In comparison with the ENGLER monographs on Africa, the Balkan volume is somewhat sparingly illustrated, and almost wholly by reproductions from photographs; the few illustrations, however, are excellently chosen.

XII. THE PERUVIAN ANDES

This volume is the second one of the series to treat of American vegetation. The general plan of the other volumes is followed, though the consideration is mainly floristic, very little being said regarding the formations.[4] WEBERBAUER, the author of the treatise, has spent several years of study in Peru, and is known to plant geographers by various papers dealing with Peruvian vegetation. Following the usual bibliography of literature and an account of the topography and climate, there is a survey of the plant families represented. Most of the volume is devoted to a detailed account of the vegetation by "zones," that is, by altitudinal subdivisions. These subdivisions are the Misti zone (2200–3400 m.) and the Tola zone (3400–4300 m.) on the western slope in southern Peru, the Loma zone of the coast, the northern desert zone, the central Sierra zone, the northern Sierra zone, the high

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[3] ENGLER, A., und DRUDE, O., Die Vegetation der Erde. XI. ADAMOVIĆ, L., Die Vegetationsverhältnisse der Balkanländer (Möische Länder) unfassend Serbien, Altserbien, Bulgarian, Ostrumelien, Nordthrakien, und Nordmazedonien. pp. xvi+567. *maps 6. pls. 41. figs. 11.* Leipzig: Wilhelm Engelmann. 1909. *M* 40 (subscription *M* 30).

[4] ———, Die Vegetation der Erde. XII. WEBERBAUER, A., Die Pflanzenwelt der peruanischen Anden. pp. xii+355. *maps 2. pls. 40. figs. 63.* Leipzig: Wilhelm Engelmann. 1911. *M* 28 (subscription *M* 20).

Andes or Puna with its wonderful xerophytic forms, the eastern sclerophyll forests, the northern Paramo, and the luxuriant eastern tropical forests. This part of the work is rather fully illustrated by excellent cuts and photographic reproductions. A short section follows on the culture plants, the volume concluding with an account of the geological development of the Peruvian flora, mostly in the form of tabulations.—H. C. COWLES.

Plant life of Maryland

"The plant life of Maryland"[5] is the title of a volume issued as a Special Publication of the Maryland Weather Service, and is one of a series of reports of unusual completeness and excellence. The first of these reports dealt with the physiography and meteorology of the state; the second with the climate and weather of Baltimore and vicinity; and this, the third volume, presents the plant life in its relations to the physiography and climate, also inquires into the correlations between natural vegetation and crop possibilities, and includes the agricultural features and forest resources of the state.

The main part of the volume is by SHREVE, who directed the botanical survey. His introduction summarizes the geography, climatology, topography, mineralogy, and soils of Maryland. In Part II, after a brief history of field botany in the state, he discusses the floristics according to the present knowledge of the flora, comparing the three zones (coastal, midland, and mountain) with respect to the number and species of plants, and the floristic relations of the zones to each other and to other regions.

Part III occupies the body of the book and presents the ecological plant geography. SHREVE considers first the eastern shore district of the coastal zone under the several divisions: upland, swamp, marsh, aquatic, dune, and strand vegetation. Comparison of this district with the coastal plain of New Jersey and of the southern states brings out striking variations. CHRYSLER treats the western shore district of the coastal zone under the following topics: forests (upland, lowland, and cypress swamps), marshes (fresh and salt), peat bogs, strand, and cultivated plants, the chief interest being in his discussion of the succession of the forest types and in the transition of salt to fresh water marshes, this region affording unusual opportunities for such studies. In the lower district of the middle zone, the vegetation is classified by SHREVE according to the soil types, the topographical and general physical conditions being here uniform, and the vegetation less diversified than elsewhere. The upper district of the midland is divided into four natural belts of ridges and valleys, and the characteristic plant life of these divisions is discussed by BLODGETT. SHREVE describes the mountain zone under seven headings: slopes,

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[5] SHREVE, FORREST, CHRYSLER, M. A., BLODGETT, FREDERICK H., and BESLEY, F. W., The plant life of Maryland. 4to. pp. 533. *pls. 39. figs. 15.* Baltimore: Johns Hopkins Press. 1911.

ridges, valleys, rocky slopes, glades, swamps, bogs, the topography determining in each case the character of the vegetation.

In Part IV, on the "Relation of natural vegetation to crop possibilities," SHREVE concludes that only in a general way may the native or introduced plant cover, as seen today, be significant of agricultural capabilities, although there is evidence that the virgin forest did give indication of the character of the underlying soil which was observed to advantage by the early settlers. Part V, on the "Agricultural features" by BLODGETT, Part VI on the "Forests and their products" by F. W. BESLEY, and Part VII, a "List of plants collected or observed" by SHREVE, complete the book.

The careful work of the authors and the collection of the floristic and ecological data make this a valuable treatise of its kind. It is handsomely printed and abundantly illustrated. For regions presented in such detail and with many local references, the lack of adequate maps is often noticed.—LAURA GANO.

MINOR NOTICES

Wettstein's Handbuch.—The mere fact that a second edition of a book has become necessary indicates that it has met some need. The second edition of WETTSTEIN'S *Handbuch*[6] does not differ essentially from the first edition. Minor inaccuracies have been corrected, additions have been made both from the rapidly increasing literature and from the author's own investigations, and a large number of illustrations, of the same high grade which made the first volume useful, have been added. As in the first edition, the work on angiosperms is particularly extensive, occupying about one-half of the entire book. This part of the work presents a compact, profusely illustrated account of all the more important families, which should give the beginner a sound foundation for advanced work, and which cannot fail to be helpful even to the professional taxonomist. It is encouraging to note that in discussing the phylogeny of angiosperms, the monocotyls are derived from the lower dicotyls.—CHARLES J. CHAMBERLAIN.

Ornamental shrubs.—It is safe to predict that the latest handbook by APGAR,[7] while intended for the general public, will prove most useful to the teaching botanist who has occasion to draw much of his material from parks and greenhouses. In its scope the volume includes not only native and hardy shrubs, but also introduced forms, many of which are conservatory plants in the northern United States. Numerous keys, based mostly upon leaf characters, appear to be most efficient in aiding the student to identify

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[6] WETTSTEIN, R. V., Handbuch der systematischen Botanik. 2d edition. 8vo. pp. viii+914. *figs. 600*. Leipzig: Franz Deuticke. 1910. *M* 24.

[7] APGAR, AUSTIN C., Ornamental shrubs of the United States. 12mo. pp. 352. *figs. 621*. New York: American Book Company. 1910. $1.50.

species even when they are not in flower. The keys are supplemented by simple descriptions and by more than 600 illustrative drawings, while a glossary of botanical terms will prove useful to the beginner, and the size of the book will recommend it to all as a most useful pocket aid to the study of a comparatively unknown portion of our flora.—GEO. D. FULLER.

Dictionary of plant names.—GERTH VAN WIJK,[8] a teacher in the schools of Holland, has published the result of a most laborious compilation of data, extending through twenty-five years. The dictionary is intended to enable one to find the vernacular name of a plant in four languages, provided he knows its scientific name; the four languages chosen being English, French, German, and Dutch. Two other parts are promised, which will really form an index to the first parts, and will enable one to find the scientific name of a plant if he knows the vernacular name in any one of the four languages. All questions as to the usefulness of such a work are submerged by amazement at this exhibition of enjoyment in endless drudgery.—J. M. C.

Album of thallophytes.—The first fascicle of an album of the algae, fungi, and lichens, by COUPIN,[9] indicates that the complete work will be useful to all who are interested in the lower plants. All the genera and many of the more important species are illustrated by drawings emphasizing the features which are of importance in classification. The figures are in plates opposite the descriptions, and with the description of each species is a bibliography of the principal contributions, so that more extended information may be easily obtained.—CHARLES J. CHAMBERLAIN.

Natürlichen Pflanzenfamilien.—Parts 241 and 242 conclude the supplement to the Chlorophyceae by N. WILLE; include that to the Phaeophyceae and Dictyotales by the late F. R. KJELLMAN and N. SVEDELIUS; and begin the supplement to the Rhodophyceae by N. SVEDELIUS, who continues it in parts 243 and 244. A new genus (*Pseudolithoderma*) of Lithodermataceae is described by SVEDELIUS.—J. M. C.

NOTES FOR STUDENTS

Current taxonomic literature.—O. AMES (Phil. Journ. Sci. Botany **6**:35–56. 1911) under "Notes on Philippine orchids with descriptions of new species III" places on record additional data concerning this group of plants in the Philippines and describes 22 species new to science.—R. C. BENEDICT (Am. Fern Journ. **1**:40–42. *pl. 2.* 1911) describes and illustrates a new species of

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[8] GERTH VAN WIJK, H. L., A dictionary of plant names. 2 parts. 4to. pp. xxiv+1444. Haarlem: Published by the Dutch Society of Sciences. 1909, 1910.

[9] COUPIN, HENRI, and COUPIN, MLLE. FERNANDE, Album générale des Cryptogames (algues, champignons, lichens). Fasc. 1. *pls. 1–15.* Paris: E. Orlhac, Editor. *fr.* 2.50.

Anemia (*A. nipeënsis*) from Cuba. The same author (Bull. Torr. Bot. Club **38**:153–190. *pls. 2–8.* 1911) presents the results of studies in the fern tribe *Vittarieae*, recognizing 7 genera. Several new combinations are made and one new species of *Polytaenium* (*P. quadriseriatum*) is described from Hayti.—E. BETHEL (Mycologia **3**:156–160. *pl. 48.* 1911) describes and illustrates a new species of *Gymnosporangium* (*G. Kernianum*) from Colorado.—E. BICKNELL (Bull. Torr. Bot. Club **38**:103–133. 1911) in continuation of his studies on "The ferns and flowering plants of Nantucket" recognizes 12 species of *Rubus* and characterizes 24 hybrids in this genus.—F. BORGESEN (Bot. Tidsskir. **30**:177–207. 1910) under the title "Some new or little known West Indian Florideae II" has published critical notes on several species of the region, describes two species new to science, and proposes a new genus (*Coelarthrum*), based on *Chylocladia Albertisii* Piccone.—F. BRAND (Ber. Deutsch. Bot. Gesells. **29**:138–145. *pl. 7.* 1911) has described several new green algae collected by MISS J. E. TILDEN in New Zealand. One new genus (*Rhytisiphon*) of the Siphoneae is proposed.—A. BRESADOLA (Med. Rijks. Herb. pp. 75, 76. 1911) has published 4 new species of Polyporaceae, two of which (*Fomes subendothejus* and *F. surinamensis*) are from South America.—F. BUBÁK (Ber. Deutsch. Bot. Gesells. **29**:70–74. 1911) in an article entitled "Eine neue Krankheit der Maulbeerbäume" describes a new genus (*Dothiorelina*) from Bulgaria. The fungus is parasitic in the branches of *Morus alba*.—L. BUSCALIONI (Ann. Botany **9**:87–122. *pls. 1–4.* 1911) records several species of the Sympetalae from the region of the Amazon in Brazil and describes and illustrates new species in the following genera: *Torenia*, *Drymonia*, and *Memora*.—C. DE CANDOLLE (Rep. Nov. Sp. **9**:229–235. 1911) has published 11 new species of *Piper* from Bolivia.—A. CHASE (Proc. Biol. Soc. Wash. **24**:103–160. 1911) presents the results of further studies on the Paniceae, and includes a new species in the genus *Valota* and two in *Axonopus*. Two new genera are proposed, namely, *Homolepis*, based on *Panicum aturense* HBK., and *Scutachne*, based on *Panicum durum* Griseb.—T. F. CHEESEMAN and H. B. HEMSLEY (Kew Bull. 188, 189. 1911) have published a new genus (*Coxella*) of the Umbelliferae; the genus is founded on *Ligusticum Dieffenbachii* Hook. f.—E. CHIOVENDA (Ann. Botany **9**:51–85, 125–152. 1911) under the title "Plantae novae vel minus notae e regione aethiopica" has published several species of flowering plants and proposes the following new genera: *Tzellemtinia* of the Rhamnaceae, *Hymenosicyos* of the Cucurbitaceae, *Erythroselinum* and *Stephanarossia* of the Umbelliferae, and *Petrollinia* of the Compositae.—R. CHODAT (Bull. Soc. Bot. Genève II, **3**:125, 126. 1911) has described a new genus (*Ernstiella*) of the Myxophyceae. The alga was found in one of the parks of Geneva.—H. N. DIXON (Journ. Bot. **49**:137–150. *pl. 513.* 1911) has published several new species of Indian mosses and includes a new genus (*Hyophilopsis* Card. and Dixon) of the Pottiaceae.—S. T. DUNN (Kew Bull. 193–198. 1911) has published a new genus (*Adinobotrys*) of the Leguminosae and refers thereto four species from the Indo-Malayan region and

China. The same author in cooperation with DR. HARMS (Jour. Bot. **49**: 106–109. 1911) has proposed a new genus (*Craibia*) of the Leguminosae. The genus, as here treated, embraces nine species of trees, all of African distribution.—C. W. EDGERTON (Phytopathology **1**:12–17. *pl. 4*. 1911) under the title "Two new fig diseases" records two fungi found on the fig tree at Baton Rouge, Louisiana, one (*Tuberculariа Fici*) being new to science.—A. ENGLER (Bot. Jahrb. **46**:1–288. *pls. 1–4*. 1911) under the general title of "Beiträge zur Flora von Afrika XXXVIII," in cooperation with several noted specialists, publishes an important contribution to our knowledge of the flora of Africa. About 160 species are here published for the first time, and one new genus (*Simarubopsis*) of the Simarubaceae from central Togo is described and illustrated. The paper includes a synoptical revision of the African species of *Ficus* by J. MILBRAED and M. BURRET. These authors recognize 95 species of this genus from Africa, and a key precedes their enumeration.—A. J. EWART, J. WHITE, and B. WOOD (Proc. Roy. Soc. Victoria, N.S. **23**²:285–304. *pls. 49–57*. 1911) under "Contributions to the flora of Australia, No. 16" have described several species new to science and propose a new genus (*Sarga* Ewart) of the Gramineae.—C. E. FAIRMAN (Ann. Mycol. **9**:147–152. 1911) under the heading "Fungi Lyndonvillenses novi vel minus cogniti" has published 8 new species of fungi from the vicinity of Lyndonville, New York.—C. FERDINANDSEN amd O. WINGE (Bot. Tidsskr. **30**:208–222. 1910) record several species of fungi obtained on the WARMING expedition to Venezuela and the West Indies in 1891–92. A new species is added to *Helotium* and one to *Sterigmatocystis*. Two new monotypic genera are characterized, namely, *Myxotheca*, found on the pinnae of *Trichomanes pinnatum* from the island of Trinidad, and *Stilbochalara*, found on decaying fruits of cacao from Venezuela.—W. O. FOCKE (Rep. Nov. Sp. **9**:235–237. 1911) records 5 new species of *Rubus* from Central and South America.—R. E. FRIES (*ibid*. 211) has published a new species of *Wissadula* (*W. indivisa*) from Paraguay.—E. L. GREENE (Leafl. Bot. Obs. and Crit. **2**:121–152. 1911) has described upwards of 50 new species of flowering plants chiefly from western United States. One new genus (*Sandbergia*) of the Cruciferae is proposed. The same author (Am. Mid. Nat. **2**:73–90. 1911) under the heading "*Antennaria* in the Middle West" recognizes 13 species of this genus from the central part of the United States; of this number 7 are said to be new. A key to the species precedes their description.—R. M. HARPER (Torreya **11**:64–67. 1911) records a new *Prunus* (*P. geniculata*) from Florida.—L. L. HARTER (Mycologia **3**:154, 155. 1911) has published a new species of *Alternaria* (*A. Forsythiae*) found at Washington on living leaves of *Forsythia suspensa* Thunb.—E. HASSLER (Rep. Nov. Sp. **9**:145–160, 193–197. 1911) has published several new species and varieties of Leguminosae and Convolvulaceae from Paraguay.—F. HEDGES (Phytopathology **1**:63–65. *pl. 15*. 1911) describes and illustrates a new fungus (*Sphaeropsis tumefaciens*) from Jamaica; this fungus is said to be "the cause of the lime and orange knot."—F. HEYDRICH (Ber. Deutsch. Bot. Gesells.

29:26–33. *pl. 2.* 1911) in an article entitled "Die Lithothamnien vor Roscoff" describes and illustrates a new genus (*Squamolithon*).—R. H. Howe, Jr. (Mycologia **3**:106–150. *pls. 41–47.* 1911) under the title "American species of *Alectoria* occurring north of the fifteenth parallel" recognizes about a dozen species and records a new one (*Alectoria pacifica* Stzb.) from the Island of Guadalupe off the California coast.—G. Kükenthal (Philip. Journ. Sci. Bot. **6**:57–64. 1911) gives a synopsis of the Philippine *Caricoideae*, with a key to the species of *Carex*, 24 being listed for the Philippines, one (*C. pycnothyrsos*) hitherto unknown to science.—J. Lunell (Am. Mid. Nat. **2**:57–60. 1911) records 4 new species of Compositae from North Dakota, and (*ibid.* 90–94) under the title "New plants from North Dakota" characterizes 8 varieties of "*Laciniaria scariosa.*"—B. Mackensen (Bull. Torr. Bot. Club **38**:141–143. 1911) records 2 new species of *Opuntia* from Texas.—W. A. Murrill (Mycologia **3**:97–105. *pl. 40.* 1911) in the eighth article on "Illustrations of fungi" describes and illustrates several plants and records new species in *Omphalia*, *Inocybe*, and *Campanularius*.—J. A. Nieuwland (Am. Mid. Nat. **2**:60–65. 1911) in an article entitled "The type of the genus *Panicum*" proposes a new generic name *Chasea*, and transfers thereto several species of *Panicum*. *Panicum clandestinum* L. is taken as the type of the newly constituted genus.—L. O. Overholts (Ohio Nat. **11**:353–373. 1911) under the heading "The known Polyporaceae of Ohio" records 118 species from that state.—A. Pascher (Ber. Deutsch. Bot. Gesells. **29**:112–125. *pl. 6.* 1911) gives an account of a new tentacle-bearing chrysomonad, found growing in ditches on *Mikrospora* and *Oedogonium* at Franzensbad, Germany. The plant has been designated by the generic name *Cyrtophora* and together with *Pedinella* Wyssotzki and *Palatinella* Laut. are referred to a distinct family Cyrtophoraceae.—F. Petrak (Rep. Nov. Sp. **9**:177, 178. 1911) has published a new species of *Cirsium* (*C. Greenei*) from northern Mexico.—J. A. Purpus (Monats. für Kakteenk. **21**:50–53. 1911) describes and illustrates a new species of *Mamillaria* (*M. Sartorii*) from Mexico.—C. B. Robinson (Philip. Journ. Sci. Bot. **6**:1–33. *pls. 1–3.* 1911) presents the concluding article in his consideration of the "Philippine Urticaceae." In this paper 11 genera are recognized and to them are referred 43 species of which 13 are new. A new genus (*Astrothalamus*) is proposed, which is based on *Maoutia reticulata* Wedd.—H. H. Rusby (Bull. Torr. Bot. Club **38**:145, 146. 1911) describes a new species of *Mayepea* and one of *Morus* from Mexico.—R. Schlechter (Rep. Nov. Sp. **9**:161–166, 212–218, 281–287, 289–294. 1911) under the title "Orchidaceae novae et criticae" has published new species of orchids from different parts of the world, including several from Mexico and Central America. One new genus (*Solenocentrum*) is proposed from Costa Rica.—P. C. Standley and J. C. Blumer (Muhlenbergia **7**:44–47. *pl. 5.* 1911) have described and illustrated a new species of *Castilleja* (*C. austromontana*) from the southern Rocky Mountains.—J. Steiner (Oesterr. Bot. Zeits. **61**:177–183. 1911) had published several new species of lichens, including one (*Buellia mexicana*) from Mt.

Hinatikatl, Central America.—G. S. WEST (Journ. Bot. **49**:82–89. 1911) under the heading "Algological notes" characterizes a new genus (*Oligochaetophora*); the genus is based on *Polychaetophora simplex* West, which was found originally growing on submerged portions of various aquatic flowering plants at Donegal, England.—J. M. GREENMAN.

Cecidology.—Among the most important of the recent papers on galls is that by DENIZOT[10] on the gall of *Andricus radicis*. This gall occurs on the roots of at least three species of oaks, and appears to resemble somewhat the American twig gall caused by *A. punctatus* Bassett. The gall is plurilocular, but its histological structure is very similar to the unilocular gall caused by *A. sieboldi*. The gall is made up primarily of parenchyma tissue, and each larva is surrounded by a definite structure as follows: (1) a zone of parenchyma tissue well filled with starch and known as the nutritive zone; the starch disappears with the growth of the larva and is supplanted by tannin and oil; (2) a protective zone of scelerenchyma tissue containing albuminoids and tannin. There is a gradual transition between these two zones. The superficial part of the gall is made up primarily of cork cells whose contents are reduced to a thin layer of tannin deposited against the inner walls. The tannin exists in all parts of the gall, but is most abundant in the parts referred to above, and increases in amount with the decrease in starch. It causes a coagulation of the contents of the cells, persisting in the protective cells in the form of grains, and in the cork cells as a thin peripheral layer. The reviewer has observed similar conditions in several of our American galls.

Another exceptionally good piece of work is that of HOUARD[11] on the action of certain scale insects on the plant tissues. His studies were restricted to *Asterolecanium variolosum*, *A. thesii*, and *A. algeriense* on *Quercus pedunculariа*, *Q. sessiliflora*, *Q. pubescens*, *Pittosporum tobira* (an Asiatic plant), *Templetonia retusa* (an Australian plant). In all cases these insects cause cone-shaped swellings, and in the tip of each cone a depression in which the insect is located. The swellings are due partly to thickening of the bark and partly to a modification of the vascular bundles. The galls differ in accordance with the response of the vascular bundles to the stimulating influences of the insects; the more compact the bundle, the greater the resistance. If the bundles are compact, the hypertrophy of the medullary rays is slight and the bundles only slightly separated, thus making it difficult for the parasite to reach any great depth. In the case of *A. variolosum*, the vascular bundle responds to the action of the insect in the formation of new wood only. This new wood possesses an abnormal structure due to the sucking of the insect interfering with the normal differentia-

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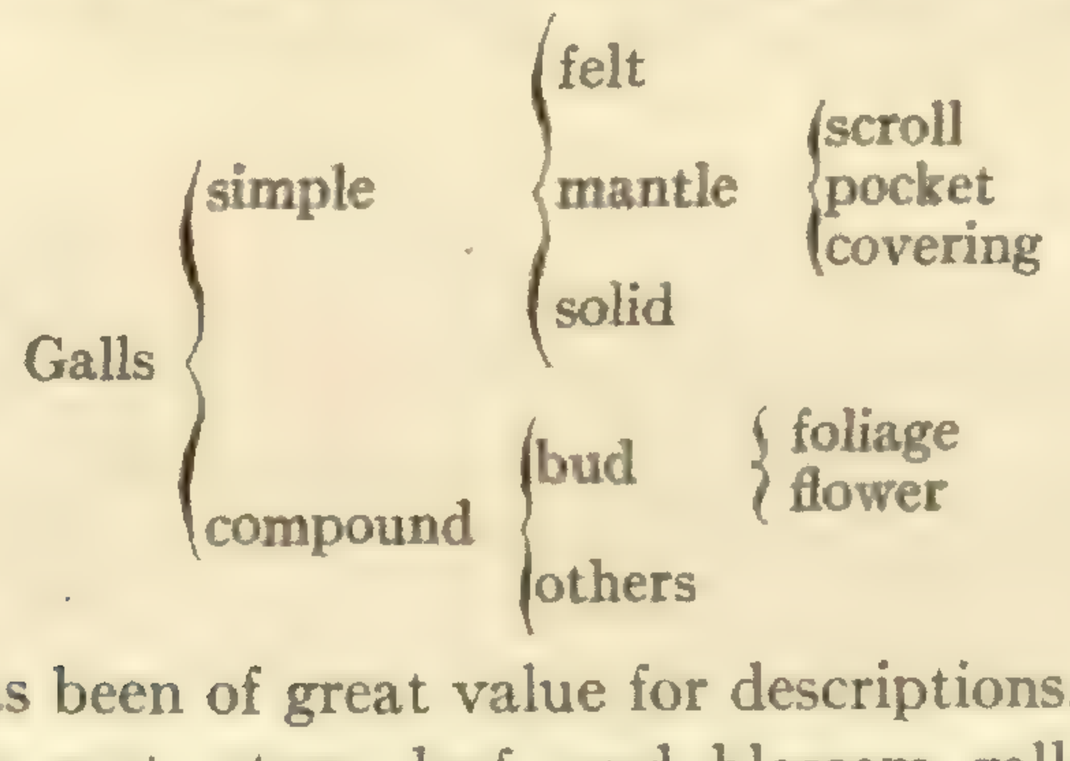
[10] DENIZOT, M. GEORGES, Sur une galle du chêne provoquée par *Andricus radicis* (Cynipide). Rev. Gén. Botanique **23**:165–175. 1911.

[11] HOUARD, C., Action de Cécidozaires externes, appartevant au genre *Asterolecanium*, sur les tissues de quelques tiges. Marcellia **10**:3–25. 1911.

tion of the fibers. The major part of this abnormal structure forms lignified cells with slightly thickened walls. In the case of *T. retusa*, the ring of vascular bundles presents enough resistance to prevent the hypertrophy of the medullary rays. However, *A. algeriense* has a stronger influence on the intermediate woody vessels, stopping their development and causing a hypertrophy of the thickened angles of the stem. The vascular bundles in the stem of *P. tobira* are much less resistant than in any of the preceding host plants; in this case the insect affects the bark, easily gains entrance to the medullary rays, and causes a hypertrophy which results in the separation of the vascular bundles. The modification of the tissues between the bundles is advantageous to the insect. In the petioles and midribs, the bundles do not form a complete ring and therefore are much less resistant than in the twigs, and are subject to much greater hypertrophy. In all cases, except the last, the external tissues of the stem undergo excessive hypertrophy and form the greater part of the gall.

The biology of galls is ably discussed by DR. ARTUR MODRY,[12] who gives a review of the subject and also the results of his own investigations. Although the study of galls is very old, it has attracted comparatively little attention from biologists. The workers on this subject have defined galls differently, but the definition given by BEYERINCK is most generally accepted at the present time. According to this definition, the gall is a "new formative growth within the body of the plant and is due to insects or plant organisms." THOMAS suggested the use of the word "cecidien" (meaning nut gall) as a substitute for all other terms; then subdivided the galls on basis of cause into Phyto-cecidien and Zoo-cecidien, and these groups into myco-, helminto-, phytopto-, entomo-cecidien, etc. Although this marked an advance in the study of cecidology, it was of very little botanical importance. This was largely overcome by KERNER,[13] who suggested the following divisions:



This division has been of great value for descriptions. In 1904 Ross suggested division into root, stem, leaf, and blossom galls. This division has been of considerable value, but was not very practical. LACAZE-DUTHIERS (1849–1853) suggested division into internal, external, and mixed galls. However, the greatest advance was made by KÜSTER, who as a result of his study

[12] MODRY, DR. ARTUR, Beiträge zur Gallenbiologie. Sechzigsten Jahresb. K.K. Staats-Realschule. 1911.

[13] KERNER AND OLIVER, The natural history of plants 2:514–554. 1895.

of gall anatomy divided them into (1) galls without cell multiplication (enlargement of cells should not be confused with multiplication of cells), (2) soft galls, and (3) hard galls. The divisions are based on the character of the tissues of which the galls are composed. The author admits there are so many intermediate stages as to make these divisions in some cases very unsatisfactory. MODRY follows KÜSTER'S divisions, and gives a very comprehensive review of the various structural (both external and internal) characters of the various groups of zoo-cecidia. A review of this part of the paper would require entirely too much space and is entirely unnecessary for those who are familiar with the literature of the histology of galls.

Another paper of great interest to Americans is by TROTTER[14] on a collection from Washington, Oregon, Arizona, California, Hawaii, and Mexico. In this paper the author describes 88 species, of which 9 have been described. Of the remaining 79, 13 are given specific names and the remainder assigned to genera only. This paper is a most excellent illustration of our lack of knowledge of the American cecidia.

Dr. SCALIA[15] gives a very interesting discussion and description of a new species on *Cyclamen neapolitanum*, to which he assigns the name *Phyllocoptes Trotteri*.

One of the most valuable contributions to American cecidology in recent years is SMITH'S[16] paper on crown gall and sarcoma. In his recent bulletin on crown gall, Dr. SMITH calls attention to the resemblances of crown gall of plants to malignant animal tumors, especially to sarcoma. This resemblance has attracted the attention of many workers, but it remained for SMITH to demonstrate that it is something more than superficial. The questions previously unsolved which SMITH answers are (1) the presence of bacteria in the secondary tumors, (2) the origin of the secondary tumor from the primary to which it remains attached by strands of tumor tissue, (3) the structure of the secondary tumor is the same as that of the primary. The strand of tumor tissue connecting the galls works its way as an outgrowth from the primary gall, through the interior of the stem and leaves. At suitable places it undergoes enlargements, forming deep seated secondary galls which eventually become apparent on the surface. These tumor strands contain the bacteria which cause the disease. We are promised another bulletin on this interesting subject which we will await with great interest.

Another very interesting contribution, which the reviewer believes should

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[14] TROTTER, A., Contributo alla Conoscenza delle Galle dell America Nord. Marcellia **10**:28–61. *pl. 1. figs. 21.* 1911.

[15] SCALIA, DR. C., Nuova Species di Eriofide sul *Cyclamen neapolitanum* Ten. Marcellia **10**:62–64. 1911.

[16] SMITH, ERWIN F., Crown gall and sarcoma. Circular No. 85. U.S. Bureau of Plant Industry. 1911.

be included under cecidology, is that part of the work of EAST and HAYES[17] on inheritance in maize which refers to "plant abnormalities." In this part of the work, the authors state their objects as follows: "The first object was to see whether the manner of transmission of inheritable monstrous characters gives any clue to the reason why monstrosities have seldom obtained a foothold in nature when in competition with normal types. The second object was commercial. If teratological specimens appear in commercial varieties of maize, it is desirable to know the easiest method to destroy them." The authors discuss the appearance of and experiments with dwarf forms, irregularity of rows of seeds on cob, bifurcated ears, ears with lateral branches, plants with striped leaves, and hermaphrodite flowers. They call attention to the fact that many of these monstrous variations occur in strains that have been self fertilized for several generations, and suggest that inbreeding may give the same effect as lack of nutrients, while cross-breeding may give the opposite effect. Monstrosities are due to retardation or acceleration of cell divisions. The question is then raised as to whether the monstrosities might not be due to an abnormal distribution of the chromatin. Another paper is promised on the effects of inbreeding in maize.—MEL. T. COOK.

Recent papers on Phytomyxaceae.—MAIRE and TISON[18] have published a brief note on *Tetramyxa parasitica* Goebel, which produces galls on *Ruppia* and *Zannichellia*. The parasite appears in the host cell in the form of an amoeba, which undergoes division simultaneously with the host cell in such a way that at first only a single amoeba appears in each cell. During this stage the nuclei are said to divide in the manner described by NAWASCHIN and by PROWAZEK for *Plasmodiophora*. As these accounts differ somewhat as to detail, it may be inferred that the division in its main features follows the method common to the members of this group, by the formation of a chromatic ring around a karyosome, both of which divide. This stage is followed by the chromidial stage, during which the chromatin disappears from the nuclei and chromatic bodies appear in the protoplasm. Later the (same) nuclei appear with a chromatin network and undergo two karyokinetic divisions, which are followed by spore formation. Karyogamy was not observed.

In a second paper, MAIRE and TISON[19] describe a new genus, *Ligniera*, to include those species of the Plasmodiophoraceae which lack the schizogenous stage or have it very poorly developed, and which do not cause gall formation in the host plant. By these characteristics the genus is separated from the genera

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[17] EAST, E. M., and HAYES, H. K., Inheritance in maize. Conn. Agric. Exp. Station, Bull. 167. pp. 129–137. 1911.

[18] MAIRE, RENÉ, et TISON, ADRIEN, Sur quelques Plasmodiophoracées. Compt. Rend. **150**: 1768–1770. 1910.

[19] ———, Sur quelques Plasmodiophoracées non hypertrophiantes. Compt. Rend. **152**: 206–208. 1911.

Plasmodiophora, *Sorosphaera*, and *Tetramyxa*. The new genus includes *L. radicalis*, which is new, *L. Junci* (Schwartz) (*Sorosphaera Junci* Schwartz), and *L. verrucosa*, also new.

OSBORN[20] gives an account of the development of the interesting form *Spongospora subterranea*, causing the corky scab of potatoes. Penetration of the organism into the host cell was not observed, nor was it possible to infect sound potatoes with spores. The first stage observed consisted of an amoeba containing a single nucleus, which had a membrane, chromatic granules, and a deeply staining karyosome. In the early stages nuclear division is followed by division of the amoeba, so that a number of independent amoebae are found in the same host cell. The parasites occur in the cambium, and when the parent cell divides, one or more amoebae are included in each daughter cell, in the manner described by NAWASCHIN for *Plasmodiophora*, and by BLOOMFIELD and SCHWARTZ for *Sorosphaera*. The division of the nuclei during this stage is of the type characteristic of the group. The chromatin forms a ring around the karyosome; both the ring and the karyosome then divide, and the halves move toward the poles, where the halves of ring and karyosome unite into a deeply staining mass. The nuclear membrane constricts between the masses, and finally divides at the point of constriction, leaving each chromatic mass enclosed in a separate membrane. No fibers or polar radiations were observed. At a later stage many of the amoebae are multinucleate, and when the food content of the host cell is exhausted, the amoebae coalesce to form a plasmodium. At this time the chromatin of the nuclei disappears and chromatic material appears in the protoplasm. When the nuclei appear organized again, they contain a chromatin network but no karyosome. The author is inclined to believe that the new nuclei are constructed *de novo*. This stage is soon followed by fusion of nuclei in pairs, and a period of nuclear growth previous to spore formation. Two karyokinetic divisions take place, after which the protoplasm is rounded up into uninucleate spores.

In a later paper MAIRE and TISON[21] give the results of further observations on *Sorosphaera*, *Tetramyxa*, *Ligniera*, and *Mollierdia*, some of which differ in some points of their development from other forms of this group. *Tetramyxa parasitica* has multinucleate plasmodia during the phase representing the schizogenous stage, the nuclear divisions not being accompanied by cell division. The chromidial stage, prominent in other forms, is lacking here. At the beginning of spore formation, the plasmodia break up into uninucleate masses. These masses become four-nucleate as a result of two mitotic divisions, and divide by constriction into four uninucleate spores. In this form, as

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[20] OSBORN, T. G. B., *Spongospora subterranea* (Wallroth) Johnson. Ann. Botany **25**:327–341. *pl. 27*. 1911.

[21] MAIRE, RENÉ, et TISON, ADRIEN, Nouvelles recherches sur les plasmodiophoracées. Ann. Myc. **9**:226–246. *pls. 10–14. fig. 1*. 1911.

well as in *Sorosphaera*, amoebae are carried into new cells by the division of the infected host cell as described above for *Spongospora*.

Ligniera radicalis develops in the root hairs and cortical parenchyma of the roots of *Callitriche stagnalis*. As stated in the former paper, a true schizogenous phase is lacking. As in *Tetramyxa*, cell division does not accompany nuclear division during the growth of the organism. The chromidial stage occurs here as usual before the meiotic divisions. The first of these divisions often occurs before the plasmodium has broken up, but in such cases the plasmodium breaks up into "energids" during the second mitosis in such a way that the four nuclei resulting from the two mitoses are inclosed in the protoplasmic masses, which break up into four spores. The mode of development of *L. Junci* and *L. verrucosa* is similar to that of *L. radicalis*.

Molliardia is described as a new genus to include *Tetramyxa Triglochinis* Molliard. This form is peculiar in producing no spores on the host plant. The infected cells contain plasmodia which soon break up into uninucleate schizonts. These become 2–8-nucleate and break up anew. The full life history of this form is not known. In conclusion, the author adds some observations on the affinities of the Plasmodiophoraceae. He is inclined to regard them as being more closely related to such forms as *Rhizomyxa* and *Woronina* among the Chytridiales than to the Myxomycetes.—H. HASSELBRING.

The Grigna mountains.—The Grigna group of mountains includes some 60 square miles of mountainous country in northern Italy, adjoining the eastern shores of Lake Como and the connecting Lake Lecco. Its phytogeographical description by GEILINGERE[22] has an additional American interest because of the location of the region near the main route of American tourist travel. Notwithstanding its small area, the elevation varies from 199 meters at Lake Como to 2,410 meters on the highest of the peaks. This permits a wide range in climate, which is of course reflected in the vegetation. The Mediterranean province does not reach so far north, but many species of Mediterranean origin are present, and the olive extends to a maximum altitude of 490 meters. Most of the area is comprised within the submontane region, with forests of oak, hop hornbeam, and chestnut extending up to 1050 meters. From this elevation to 1650 meters the montane beech forests dominate. These in turn are succeeded by the subalpine forests of larch as far as 1950 meters, above which is the treeless alpine region. For all of these regions the author distinguishes ecological groups with a detail seldom approached in America. He recognizes seven chief types of vegetation, including forest, bush-forest, perennial herbs, grassland, swamps, aquatic vegetation, and rock vegetation. These are subdivided into formational groups, formations, and societies, of successively minor importance. This classification is based

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[22] GEILINGERE, G., Die Grignagruppe am Comersee. Bot. Centralbl. **24**[2]: 119–420. 1909.

primarily upon physiognomy, and only secondarily upon environment or floristic composition. It is doubtful whether such a method can ever give entirely satisfactory results, although the author considers it the best for this region, where all the associations show the effect of cultural changes. Probably the gravest defect of the paper is the entire failure of the author to discuss the dynamics of the vegetation. The development of the various associations and their successional relations are omitted completely. Illustrations would have added greatly to the clearness of the descriptions, and the scale of the accompanying map would have easily permitted the location of the chief types of vegetation. Almost half of the lengthy article is occupied by a carefully annotated list of species.—H. A. GLEASON.

Gametophytes and embryo of Pseudolarix.—MIYAKE and YASUI[23] have investigated the monotypic *Pseudolarix* (*P. Kaempferi*), a native of China, one of the Abietineae whose morphology had not been studied. The material was obtained from a tree growing in a garden in Pallanza, Italy. The winged pollen grains contained the usual cells of the male gametophyte, and the divisions showed 12 chromosomes, but the later development of the gametophyte was not seen. Megaspore formation was observed, a linear tetrad being formed about the time of pollination (April in Italy). The large central vacuole is formed in the spore stage (before free nuclear division), and the young female gametophyte is invested by several layers of nutritive cells. At maturity, the megaspore membrane is well developed, as in other Abietineae. Early in June the female gametophyte is solid tissue, and then the 5 or 6 archegonium initials appear, the archegonia maturing in about three weeks. After the division of the central cell, the ventral canal cell disorganizes at once. Fertilization occurs about the end of June, and the first four free nuclei of the proembryo move to the base of the egg, walls appearing with the next division. The cells of each tier divide, and the completed proembryo consists of four tiers, with four cells in each tier. The functions of the tiers are as in *Pinus*, and the whole situation seems to be an almost exact duplication of that genus.—J. M. C.

A cedar bog in Ohio.—DACHNOWSKI[24] records, as an isolated area of northern plants, left behind in the great northward migrations following upon the retreat of the ice sheet of the glacial period, a swamp in central Ohio, characterized by *Thuja occidentalis* and other species not usually found south of central Michigan. Mats of sphagnum, together with the sundew and various orchids, testify to the true bog character of the association.—GEO. D. FULLER.

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[23] MIKAYI, KÜCHI, and YASUI, KONO, On the gametophytes and embryo of *Pseudolarix*. Ann. Botany **25**:639–647. *pl. 48*. 1911.

[24] DACHNOWSKI, ALFRED, A cedar bog in central Ohio. Ohio Naturalist **11**:193–199. 1911.

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December 1911

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VOLUME LII NUMBER 6

THE
BOTANICAL GAZETTE
DECEMBER 1911

LIGHT INTENSITY AND TRANSPIRATION[1]

BURTON EDWARD LIVINGSTON

(WITH ONE FIGURE)

Introduction

While it is well known that light intensity plays an important rôle in the determination of water loss from plants, our knowledge of this matter is purely qualitative. The present paper deals with an attempt to find some simple means of physically determining the intensity of solar radiation with reference to its effect on plant transpiration. While the results to be here brought forward do not possess that degree of completeness that we are wont to expect in the fields of physics and chemistry, yet they emphasize the quantitative aspect in the study of the external factors which influence plants in the open, and they seem to place in the hands of ecologists of a quantitative turn of mind a somewhat ready means of approximating the physical magnitude of one of the most important, and at the same time most baffling, of the environmental conditions with which they have to deal.[2]

The total amount of transpirational water loss from a plant, for any given period, may be considered as a summation of the effects of the evaporating power of the air and of the radiant energy absorbed throughout the period, modified by certain secondary

[1] Botanical Contribution from the Johns Hopkins University, No. 21.

[2] The pressing need for methods of evaluating the various external factors which affect plants has been emphasized in a paper read before the Botanical Society of America in 1908. See Plant World **12**: 41–46. 1909; and Amer. Nat. **43**: 369–378. 1909.

effects of these conditions and by certain responses to other conditions. One secondary effect of variations in light intensity is seen in the opening of stomata when many plants are transferred from darkness to diffuse or stronger light. These openings close, or tend to close, in many plants when light gives place to darkness or to very dim light. But there seems to be no evidence for thinking that stomatal movement is at all marked as long as the intensity of illumination is above a certain minimum, about what is known as weak diffuse light. Of course they close with wilting under any light conditions (see LLOYD, *Publ. 82* of the Carnegie Institution).

Another secondary effect of high evaporation conditions, whether caused by direct sunlight or by dryness of the air, etc., is the removal of water from the leaves at a rate more rapid than its rate of entrance, so that the cells are plasmolyzed and general wilting occurs. It is probable that this effect is felt long before actual wilting is to be observed; whenever transpiration surpasses the rate of water supply to the transpiring tissues it must be supposed that a gradual lowering of the vapor tension of the water films held in the moist cellulose walls will ensue, just as a semi-dry piece of filter paper will exhibit a much lower vapor tension than a similar piece saturated. Long before plasmolysis occurs we should expect to find that the capillary menisci of the cell membranes abutting upon the internal atmosphere of the leaf would become more and more concave, and would perhaps break and retreat into the pores of the membrane. In the one case, the vapor tension of the water film, in the other their actual superficial extent should be reduced. It may thus come about that an increase in the evaporating power of the air or of solar insolation might produce, by its very accelerating influence, a retardation in the transpiration rate. Such a phenomenon is common in soils, where an increase in the rate of water loss above the rate of diffusion of water to the soil surface causes the water films to retreat into the soil and thus *decreases* the rate of water loss. It is thus that the "dust mulch" is produced, by which *adaptation* the soil seeks to reduce water loss in a dry time! A measurable falling off in the relative transpiration rate, occurring in the forenoon, when the evaporating power of the air and the light intensity are both still increasing in their daily march,

is exhibited in certain of the transpiration graphs of *Publ. No. 50* of the Carnegie Institution. These occurrences may well be due to the phenomenon just suggested, which may be termed *incipient wilting*. If the process were carried far enough, actual wilting would of course ensue. If incipient wilting be the true cause of this sort of fall in transpiration, without any appreciable stomatal closure, it should make itself manifest by a gradual fall in the gross water content of the leaves themselves, which should become more marked as evident wilting was approached. It is seen, then, that either stomatal closure or this hypothetical incipient wilting must act to decrease the equivalent evaporating surface of plants. By equivalent evaporating surface is here meant a free water surface which would evaporate the same amount of water as the plant, at the same place and for the same period.

Since the secondary effects of variations in light intensity through the photosynthetic process may be safely regarded as negligible in the present state of our inquiry, they will not be considered here. We may therefore assume that (for short periods having light intensities continuously adequate to prevent the closure of stomata, and with transpiration rates and a moisture supply which do not produce incipient wilting) the plant is virtually to be looked upon as an *integrating atmometer*, automatically summing the various increments of water loss from moment to moment as these fluctuate in magnitude. It might therefore be expected that a physical atmometer exposed at the side of a plant should exhibit the same march of the evaporation rate as that evidenced in the transpiration of the plant, providing of course that suitable corrections of the observed rate be applied, to adequately account for any and all internal changes in the organism which were influential in reducing the effective or equivalent evaporating surface of the latter. It is on this general supposition that the methods used in this study are based.

To keep logically and spatially within bounds, I shall here consider the effects of changes in the intensity of illumination between strong diffuse light and direct sunshine, thus once for all avoiding the question of marked stomatal movement. The stomata in my

experiments are supposed to be open, in the day condition, throughout. I shall also limit my considerations to short periods of time, at least to short periods in strong light, thus aiming at an avoidance of the problem of incipient wilting as above set forth. The former of these problems has been touched upon already (see *Science* N.S. **29**:269–270. 1909), and the full consideration of it should make another title. The second problem, of incipient wilting, cannot be experimentally considered at the present time.

The specific problem which now holds our attention is, then, Is it possible by any simple means to estimate quantitatively the various light intensities to which plants in the open are subjected and so to sum the effects of these as to be able approximately to calculate the variations in transpiration thus brought about, and the total transpiration for the longer period in which these variations occur? It is obvious that the solution of such problems as this is of the utmost importance in establishing a basis for a scientific agriculture. Also, such problems lie at the bottom of considerations of the factors determining plant distribution, and it must be through their solution that ecology may at length emerge from the descriptive and classificational stage in which, for the most part, it now finds itself. The importance of our present inquiry is exceeded only by its difficulty.

Apparatus and methods

To attack the problem outlined above it was necessary to measure the water loss from experimental plants under different light intensities, and to compare the various rates thus obtained with readings taken, for the same periods and exposures, upon whatever physical instruments were available for the estimation of light intensity. For the plants, the ordinary method of weighing potted and sealed specimens was resorted to. A number of different instruments for determining light intensity were tested. I shall proceed first to a discussion of these instruments.

Since the intensity of solar radiation varies from time to time, even for short periods, as on a partly cloudy day, our great desideratum in the present connection is an instrument or method for automatically obtaining an integration of this factor for a given

time period. One such device was available at the inception of this work, another was devised.

1. The Hicks solar radio-integrator (obtainable from J. HICKS, Hatton Garden, London) consists of a glass vacuum chamber, the upper portion of which (a spherical bulb) is about half filled with dark-colored alcohol and exposed to the light. The alcohol vapor produced by the absorption of energy by the dark surface is condensed in a lower bulb and collected in a still lower burette-like, graduated tube. The condenser and receiver are shaded during operation, and readings are obtained from time to time on the amount of alcohol distilled into the tube. The instrument is occasionally to be inverted and the collected alcohol replaced in the exposed bulb, an operation made possible by a bent tube connection between the two bulbs. The rate of distillation depends of course on the difference between the vapor tension of the alcohol in the upper bulb and that obtaining in the shaded part of the apparatus. The shaded part nearly maintains the temperature of the surrounding air, while the exposed bulb tends to be warmed by the sunshine. Thus this instrument causes the sun's rays to perform work in vaporizing alcohol and furnishes a means of measuring the work accomplished in terms of the amount of the liquid accumulating in the graduated tube. It is thus seen to be self-integrating.

2. Various lines of experimentation had shown that the porous cup atmometer, a self-integrating device for estimating the evaporating power of the air (see *Publ. No. 50* of the Carnegie Institution), is measurably affected by sunshine; that, *ceteris paribus*, it loses more water in direct sunlight than in shade. The difference in rate so produced, however, is not as great as that observed in plants under the same varied conditions of illumination. Considering this fact, it occurred to me that it should be possible to modify the porous cup in such manner as to cause it to absorb a greater proportion of the sun's energy, and thus render the ratio of its readings in light and shade more nearly like those obtained from the plant. The instrument already integrates the influx of energy, in terms of the amount of water evaporated, and the contemplated alteration should involve only the coloring of the porous evaporating surface so as to increase its power to absorb radiant

energy. After numerous preliminary tests this possibility was achieved.

The porous cups are now furnished in a dark-colored clay, a deep, grayish brown, and these cups show a marked increase in light-absorbing power over the ordinary white ones.

3. Another light-absorbing cup was obtained by coating the white form with a thin layer of washed lampblack. Common lampblack is boiled in distilled water, allowed to cool and settle, and the water decanted as well as possible. This process is repeated three to five times, and furnishes a clean, insoluble, and impalpable black powder, in the form of an aqueous paste. The latter may be diluted and applied to the cups with a small brush. This application should be made *after* the cup is filled and ready for operation, as the absorption of water by the surface when thus arranged is sufficient firmly and quickly to fix the carbon layer in place, and the latter is never allowed to become drier than it is destined to be in the actual operation of the instrument. The cup cannot be handled by the coated surface without injury, but it is a simple matter to renew the coating if such injury occurs. These coated cups operate in essentially the same manner as the permanently colored ones. As used in these tests, the white, brown, and black cups were installed on burettes, essentially as figured in *Publ. No. 50* of the Carnegie Institution.

4. The black bulb thermometer *in vacuo* (the one used was obtained from the Kny-Scheerer Co., New York) is essentially an ordinary glass-mercury thermometer, the bulb of which is blackened and inclosed in a thin glass vacuum bulb. It is exposed to the light for a short time period and the rise of the temperature of the bulb noted as the reading. The instrument must be shaded and must come to air temperature between observations. It is seen that the light absorbed by this instrument is made to do the work of expanding the mercury, the amount of expansion occurring in a specified time being the measure of the energy absorbed.

The devices for light estimation thus far mentioned all depend upon the *heating* effect produced by the absorbed light. Another group of instruments, all following the principle of the Bunsen-Roscoe "photometer," depend upon the chemical effect produced

by the absorbed rays. These instruments now make use of some form of photo-sensitized paper, and the reading is either the length of time required to produce a certain standard shade of color in the paper, or the depth of color produced by an exposure of a certain length. WIESNER'S instrument (see his *Lichtgenuss der Pflanzen*) belongs to this class. They are not photometers in any true sense, but really actinometers, measuring only the actinic effect of the light. The paper may be modified so as to give sensitiveness in any part of the spectrum, but the region to which they are sensitive is always rather limited, and the sensitiveness is not uniform throughout this region. Another obstacle in their operation comes from the difficulty of procuring proper standard colors; a third arises from the fact that the comparison of the color produced with the standard depends to a great extent upon the observer's judgment, the sensitiveness of his retina, etc. Two forms of actinometer were tested in this work. They were exposed to the action of the light till the sensitive paper attained the shade of the standard, the record being made in seconds.

5. The simplest form of actinometer for our estimations is the Wynne exposure meter, for sale by most dealers in photographic goods. It is very convenient to use, the paper therefor is apparently carefully standardized, and with each package of paper is furnished a slip of non-fading standard color suited to that particular lot of paper.

6. The other instrument of this class to which we had recourse is the Clements actinometer, a modification of the Wiesner type of instrument, using any form of photographic paper which the user may wish. It is described by CLEMENTS in his *Research methods in ecology*. As there recommended, I used "solio" printing out paper, and made my own standard color (water colors, afterward varnished), which was no easy task. As will be shown in the records of these tests, there is no doubt that this method is as satisfactory in operation as that of the Wynne, but the former is somewhat more difficult. I have had evidence, moreover, that the "solio" brand of paper is rather more apt to alter with age (at least in a warm climate) than the Wynne paper.

Since all of these instruments, both thermal and actinic, depend

for their records upon the absorption of incident radiations, it is essential that the angle of incidence of the impinging light be always the same. But the direction of incidence of the sun's rays is constantly changing throughout the day, and varies, for the same hour, from day to day. It is therefore necessary to consider this matter in the operation of any and all forms of absorbing instruments. The Hicks instrument cannot be adjusted in this regard, for the main absorbing surface is the meniscus of alcohol in the upper bulb.

The porous cup atmometer possesses a cylindrical absorbing surface, modified slightly at the closed end of the cup, which latter part may readily be removed from operation by a suitable covering if desired. I am convinced that the error involved from the curved end of the cup, however, is negligible in this sort of estimation. The form of cup used was the usual one, the modification recently described by TRANSEAU (BOT. GAZ. **49**:459. 1910) would no doubt be as efficient for our purpose. To receive the sunlight always at the same angle, the cups are so placed that their long axis is perpendicular to the direction of light incidence at noon, the common plane of sun and cylinder being vertical. When so arranged the sun virtually rotates about the cup, its rays always illuminating one-half of the surface only, and falling always vertically upon a longitudinal line through the center of the lighted area. The position of the lighted area on the cup is constantly changing, but since all sides of the cup are supposedly equivalent, this introduces no complication. The position of the instrument will of course vary with the sun's altitude, that is, with latitude and season, but may readily be determined from an almanac or by simple observation at high noon. Actual tests showed clearly that the vertical cup, as ordinarily used, fails to record proper intensities of sunshine at and about noon, for at that time only a small portion near the tip receives perpendicular radiation. Of course in high latitudes the vertical position would not introduce so great an error as nearer the equator, and the error in winter would be less than in summer. The black bulb thermometer is to be exposed in the same way as the cups.

The photographic papers were always exposed by hand, so placed

that they received perpendicular rays from the direction of the sun at the time of observation.

As to the portion of the entire radiation which is absorbed by these various instruments, it is possible to say very little at the present time. It is fairly certain that portions of all the various wave-lengths of light, as well as of the infra-red and ultra-violet, are absorbed by the thermal instruments. On the actinometers we may be as certain that little effect is produced outside the actinic rays. Since the heating effect is the one which we are interested in at present, because our inquiry deals with the evaporation of water from green leaves, it is obvious that on a-priori grounds the thermal instruments are to be regarded as the most reliable. The quantitative statement of this whole matter must be left to some future time.

One other theoretical point may be mentioned here with reference to the interpretation of the results obtained with these instruments. It must be borne in mind that other factors besides radiation intensity are active in the control of evaporation, both from the porous cup and from the plant. Thus, in the night time the evaporation rate and that of transpiration are by no means *nil*, while the readings of the instruments which do not deal with evaporation will vanish at that time. From this fact we may expect the differences between two light intensities as shown by the non-evaporating instruments to be much greater than those shown by the evaporating ones. The latter always record the rate *without* light influence *plus* that due to light, the former can show no rate without the influence of radiant energy. It is possible so to manipulate the porous cup as to obtain readings from it directly comparable to those from the black bulb thermometer, but this cannot be entered into here.

Experimentation

It was my good fortune to be able to spend the summer of 1910 at the Desert Laboratory, Tucson, Arizona, under auspices of the Department of Botanical Research of the Carnegie Institution of Washington. During this period, and with the assistance of Dr. WILLIAM H. BROWN, now of the Michigan Agricultural College, a number of lines of inquiry which had been previously begun were

continued, the matters considered in the present paper forming a portion of our operations. Without the enthusiastic cooperation of Dr. BROWN, the amount of experimentation and other work accomplished would have been much smaller, and the quality less satisfactory.

In the three series of tests to be presented, the plants stood upon a table in the open, the instruments being arranged in their immediate vicinity, so that the whole group of plants and instruments occupied a space perhaps 40 or 50 cm. square. Reduced light intensities were obtained by placing over the group, at a height of something less than a meter above the table, a cloth screen about a meter square, supported by a light wood frame and four light wood supports at the angles. The screen was always so placed that all the objects of the experiment were well within the shadow; they never received any direct sunshine while the shade was in position. The burettes of the atmometers and the tube of the radiometer projected below the table, so that the active portion of all instruments was always at approximately the same height from the table (and distance below the screen) as the plant foliage. The plants were 10–20 cm. in height; they had been lifted from the open soil several weeks previously and had been carefully accustomed to full sunlight. All had grown appreciably since potting, were leafy and apparently in good condition. They were in tinned sheet iron cylinders, some 8 or 10 cm. in diameter and about as high, which, during the experiments, were sealed by the application of prepared modeling clay over the soil surface and over the drainage openings at the base.

The plants were weighed and the instruments read at intervals of one-half hour, or as nearly so as possible. Where the time period was greater or less than 30 minutes, the data have been corrected to this time period. Weighings were made in the house, each plant remaining out of its proper position only long enough for this operation. In every test, after two half-hour periods of sunlight, there followed two similar periods under shade, these being in turn followed by two more periods of sunshine. The black bulb thermometer was covered most of the time by a loosely fitting cylinder or sheath of asbestos board, open at both ends to

allow air circulation. When a reading was to be taken, this sheath was removed far enough to expose the scale, and a reading of the shade temperature was taken. Then the sheath was completely removed and the rise of temperature which took place in a single minute was noted. The photographic instruments were operated by exposure in the hand, close to the plants, a stop watch being used to determine the length of time needed to produce darkening of the sensitive paper to the degree of the standard color, a bit of which was attached to the case of the instrument, directly adjoining the exposure opening. All instruments and plants had been in full sunshine for an hour or more at the beginning of an experiment. Wind velocity was taken, and shade temperatures, but since these data show no relation to the resulting transpiration ratios, they need not be reproduced here. Throughout the tests there was always some air motion and never a high wind, the velocity varying from 0.2 or 0.3 to 2.0 or 3.0 miles per hour. The temperature varied from about 30 to 35° C. The plants used were *Physalis angulata* L. var. *Linkiana* Gray, *Xanthium commune* Britton, and *Martynia louisiana* Mill. They will be referred to merely by the generic names.

Results

The first series of observations extended from 8:00 A.M. to 1:00 P.M., August 9, 1910. A plant of *Physalis*, one of *Xanthium*, and the three porous cup atmometers (brown, black, and white) made up the series of objects. During the second hour the shade used was of white "8-ounce cotton duck" or tent canvas. During the fourth hour the shade was of a single thickness of "cheesecloth." The data from this series are given in table I.

To study, in a general way, the comparative effects of shade on the rates of water loss of the different objects, it is expedient to reduce each series of figures to relative values. We may take the datum for period 4 as unity in each case, and form the new series by dividing this datum into each of the remaining data. Graphs of these derived quantities are given in fig. 1, all of them passing through the common point (unity) at period 4. These graphs are thus directly comparable as to the relative heights of their ordinates

The periods of shade are denoted on the graphs by a broad black line below.

The graphs show merely a general and qualitative agreement between the rates of water loss from the various objects. It is quite evident that the white cup fails to show nearly as great fluctuations with light and shade as do the plants. On the other hand, the brown and black atmometers agree fairly well with each other

TABLE I

Period	Exposure	Losses per 30 mins., grams or cc.				
		Physal.	Xanth.	Brn. atm.	Blk. atm.	Wht. atm.
1.....	Open	2.1	3.4	3.2	3.7	2.0
2.....	Open	3.0	4.2	4.3	4.7	2.8
3.....	Canvas shade	1.7	2.4	4.1	3.4	2.4
4.....	Canvas shade	1.7	2.4	2.1	2.9	2.4
5.....	Open	2.7	3.9	3.5	3.8	2.4
6.....	Open	5.1	4.5	4.0	5.0	3.1
7.....	Cheesecloth shade	3.0	3.2	3.3	4.0	2.9
8.....	Cheesecloth shade	1.9	3.7	2.5	3.7	2.3
9.....	Open	3.2	4.1	3.7	4.8	3.4
10.....	Open	3.5	4.2	4.1	5.3	3.5

and with the plants. The *Physalis* plant lost an inordinate amount in period 6, the brown cup lost what appears as too much in period 3, and the behavior of the *Xanthium* plant in the last three periods is unusual; otherwise the agreement in the different ordinates is about what should be expected. Attention may be called to the general ascent of the series of three maxima for two of the instruments, showing clearly the gradual increase of the sun's intensity from 8:00 A.M. to 1:00 P.M. Also, with the thinner shade neither of the plants and neither of the dark instruments exhibit such a fall in rate of water loss as they do in the denser shade. We may now turn to the quantitative relations shown by these series of data.

Since the use of two different shades really constitutes two separate tests, we may consider the observations for the first six periods as test I, and those for the last six as test II, there being a common period of sunshine for the two tests. If now we calculate the ratios of the two sun periods, respectively, in each test, to those of the shade period intervening, we shall obtain quantitative

measures of the relations which we wish to study in detail. But it is obvious that the first half-hour in any condition fails to give as clear an expression of the response to that condition as does the second half-hour, there usually being a more or less marked

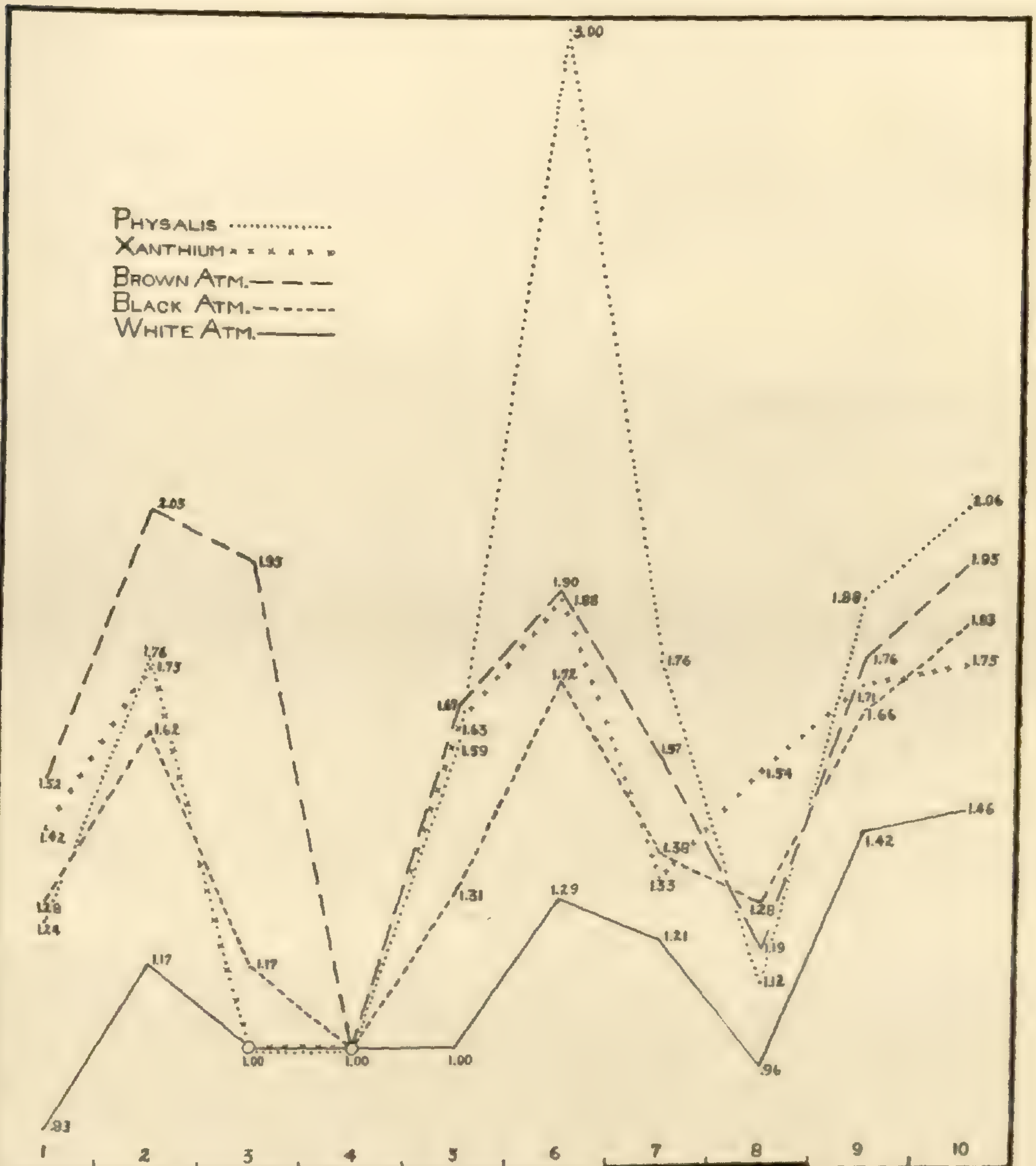

FIG. 1

lag of effect behind cause; therefore we need give attention only to the second period in each condition. Thus a period of 30 minutes is allowed to elapse after each change of conditions before use is made of the data obtained. This is a common method for the

treatment of such changes in physics as well as physiology. The two *second* half-hour periods of sunshine will be termed the *first* and *second sun exposures*, the second half-hour of shade giving us the measure for the *shade exposure*. All of the sun-shade ratios are given in table II. Examples may make the procedure of their derivation more evident. The first ratio of test I for *Physalis* is 3.0÷1.7, or 1.76. The second ratio for the brown atmometer in test II is 4.1÷2.5, or 1.64, etc.

TABLE II

		Sun-shade ratios of rates of water loss				
		Physal.	Xanth.	Blk. atm.	Brn. atm.	Wht. atm.
Test I (canvas)	1st sun exp....	1.76	1.75	2.05	1.62	1.17
	2d sun exp.....	3.00	1.88	1.90	1.72	1.29
Test II (cheesecloth)	1st sun exp....	2.68	1.22	1.60	1.35	1.35
	2d sun exp.....	1.84	1.14	1.64	1.43	1.52

If both plants were influenced alike and only by the direct heating of the sun's rays, and if the instruments were affected by radiant energy just as were the plants, that is, per unit of surface exposed, then we should expect all these ratios to be equal. In so far as they are not equal, they signify a variation in the effect produced upon the two plants and upon the three instruments by the same alterations in light intensity. Thus, if any one of these instruments were used as a basis for light measurement, to predict the influence of light changes upon either of these plants, the instrumental result must obviously be corrected. Since it is already clear that the two plants do not entirely agree in their sun-shade ratios, it will be necessary to find correction coefficients, not simply for each instrument, but *for each instrument for each plant*. From the sun-shade ratios of table II have been calculated the correction constants, by which the ratio of any instrument for any period is to be modified (multiplied) so as to equal the corresponding ratio for either plant, and these coefficients are given in table III. As an example of the method of derivation, the first coefficient of correction for the black atmometer in reference to *Physalis* (test I) is

1.76÷1.62, or 1.09. Each pair of coordinate coefficients for each test is averaged, also, in the table.

TABLE III

		Correction coefficients					
		Brown atmom.		Black atmom.		White atmom.	
		Physal.	Xanth.	Physal.	Xanth.	Physal.	Xanth.
Test I	1st sun exp...	0.86	0.85	1.09	1.08	1.50	2.33
	2d sun exp....	1.58	0.99	1.74	1.09	1.50	1.46
	Average.....	1.22	0.92	1.42	1.09	1.50	1.90
Test II	1st sun exp...	1.69	0.76	1.99	0.90	1.99	0.90
	2d sun exp....	1.12	0.70	1.29	0.80	1.21	0.75
	Average	1.40	0.73	1.64	0.85	1.60	0.83

The second series of observation (test III) was carried out from 10:00 A.M. to 1:00 P.M., August 11. The shade here used was of two thicknesses of cheesecloth. Three plants were used, one of each of the forms above mentioned, but different specimens, and one of *Martynia louisiana*. Besides the three atmometers, all of our other instruments were operated in this series. We may neglect the losses for the first half-hour periods of each exposure, since they are not to be used in calculating the different ratios. The rates of loss, or in the case of non-evaporating instruments the averages of two readings taken at the beginning and end of the second half-hour of each exposure, are given in table IV, and the corresponding coefficients of correction in table V. There was almost no discrepancy shown between the first and second readings of the non-evaporating instruments; the conditions for the half-hour were sensibly constant. In the case of the two photographic papers the ratios are of course inverted, since the light intensity must vary inversely as the time required to produce the given depth of color.

A third series (test IV) was carried out on August 12, from 10:00 A.M. to 1:00 P.M. The plants were similar to those of test III, but were different individuals; the shade was of canvas, as in test I. For this series only the final coefficients of correction and their averages need be given. They may be found in table VI.

TABLE IV

TEST III	LOSSES AND READINGS PER 30 MINUTES									
	Physal. (gm.)	Xanth. (gm.)	Martyn. (gm.)	Brown atm. (cc.)	Black atm. (cc.)	White atm. (cc.)	Integr. (cc.)	"Solio" (sec.)	Wynne (sec.)	Black therm. (deg. cent.)
1st sun exposure.....	3.45	3.98	3.12	2.9	3.7	2.2	3.00	34.5	2.4	6.7
Double cheesecloth shade.....	2.88	3.48	2.70	2.6	2.6	2.2	1.71	95.0	5.5	3.0
2d sun exposure.....	4.35	4.05	3.54	3.3	4.5	2.7	2.95	38.0	2.15	6.5

TABLE V

TEST III	COEFFICIENTS OF CORRECTION					
	Brown atmometer			Black atmometer		
	Physal.	Xanth.	Martyn.	Physal.	Xanth.	Martyn.
1st sun exposure ...	1.07	1.02	1.04	0.85	0.80	0.82
2d sun exposure....	1.19	0.91	1.03	0.87	0.67	0.76
Average.....	1.13	0.97	1.04	0.86	0.74	0.79

	White atmometer			Integrator		
	Physal.	Xanth.	Martyn.	Physal.	Xanth.	Martyn.
1st sun exposure ...	1.20	1.14	1.16	0.69	0.65	0.66
2d sun exposure....	1.23	0.94	1.07	0.87	0.67	0.76
Average.....	1.22	1.04	1.12	0.78	0.66	0.71

	"Solio" paper			Wynne paper		
	Physal.	Xanth.	Martyn.	Physal.	Xanth.	Martyn.
1st sun exposure ...	0.44	0.41	0.42	0.52	0.50	0.51
2d sun exposure....	0.60	0.46	0.52	0.59	0.45	0.51
Average.....	0.52	0.44	0.47	0.56	0.48	0.51

	Black thermometer		
	Physal.	Xanth.	Martyn.
1st sun exposure ...	0.54	0.51	0.52
2d sun exposure ...	0.70	0.53	0.60
Average	0.62	0.52	0.56

TABLE VI

Test IV	Coefficients of correction					
	Brown atmometer			Black atmometer		
	Physal.	Xanth.	Martyn.	Physal.	Xanth.	Martyn.
1st sun exposure ...	1.38	1.09	0.99	1.38	1.09	0.99
2d sun exposure....	1.53	1.26	0.97	1.46	1.21	0.93
Average.....	1.46	1.18	0.98	1.42	1.15	0.96
	White atmometer			Integrator		
	Physal.	Xanth.	Martyn.	Physal.	Xanth.	Martyn.
1st sun exposure ...	1.99	1.58	1.43	0.43	0.34	0.31
2d sun exposure....	1.23	1.68	1.29	0.69	0.57	0.44
Average.....	1.61	1.63	1.36	0.56	0.46	0.38
	"Solio" paper			Wynne paper		
	Physal.	Xanth.	Martyn.	Physal.	Xanth.	Martyn.
1st sun exposure ...	0.21	0.16	0.15	0.43	0.34	0.31
2d sun exposure....	0.25	0.21	0.16	0.51	0.43	0.33
Average.....	0.23	0.18	0.15	0.47	0.39	0.32
	Black thermometer					
	Physal.	Xanth.	Martyn.			
1st sun exposure ...	0.40	0.31	0.29			
2d sun exposure ...	0.49	0.40	0.31			
Average	0.45	0.36	0.30			

Finally, in table VII are brought together all the average coefficients from the preceding tables, together with *their* averages, for each plant for the whole investigation. This second average gives us a coefficient that may be taken to represent each instrument with reference to each plant. The average of the three different coefficients thus obtained for each instrument is given in the last column of the table. The latter average may perhaps represent the correction to be applied to each instrument for plants in general. Of course the latter statement is a pure assumption, based on the

gratuitous supposition that plants in general may be found to average up, in their sensitiveness to light intensity, as did the three which happened to be used in these tests.

TABLE VII

Instrument	Coefficients of correction					Average	
	Plant	Test I	Test II	Test III	Test IV	For plant	For instr.
Brown atm.	Physal.	1.22	1.40	1.13	1.46	1.30	1.09
	Xanth.	0.92	0.73	0.97	1.18	0.95	
	Martyn.	....	....	1.04	0.98	1.01	
Black atm	Physal.	1.41	1.64	0.86	1.42	1.33	1.06
	Xanth.	1.09	0.85	0.74	1.15	0.96	
	Martyn.	....	....	0.79	0.96	0.88	
White atm	Physal.	1.92	1.60	1.22	1.61	1.59	1.36
	Xanth.	1.48	0.83	1.04	1.63	1.25	
	Martyn.	....	....	1.12	1.36	1.24	
Integr	Physal.	....	....	0.78	0.56	0.67	0.59
	Xanth.	....	....	0.66	0.46	0.56	
	Martyn.	....	....	0.71	0.38	0.55	
"Solio" paper	Physal.	....	....	0.52	0.23	0.38	0.33
	Xanth.	....	....	0.44	0.18	0.31	
	Martyn.	....	....	0.47	0.15	0.31	
Wynne paper	Physal.	....	....	0.56	0.47	0.52	0.46
	Xanth.	....	....	0.48	0.39	0.44	
	Martyn.	....	....	0.51	0.32	0.42	
Black therm.	Physal.	....	....	0.62	0.45	0.54	0.47
	Xanth.	....	....	0.52	0.36	0.44	
	Martyn.	....	....	0.56	0.30	0.43	

Conclusions

In the last section have been brought forward the results of an experimental attempt to determine what sort of corrections must be applied to the data furnished by the seven instruments tested, in order that we may obtain from these data the sun-shade ratios of the transpiration rates as actually exhibited by the different plants. Four tests, each furnishing two sun-shade ratios for each plant, have been carried out. In all, we have eight tests for *Physalis* and the same number for *Xanthium*, but only four for *Martynia*. It is safe to assume that the full sunshine for the three days of this inquiry was approximately the same; all tests continued through

about the same part of each day. It is quite obvious that in other regions the results might have been different, but I am convinced that the present data would agree fairly well with those for the hottest summer days in most parts of the United States. It is to be remembered, however, that the work was done in the arid region, albeit in the moist season, and that humidity has not yet been investigated with reference to its quantitative effect on plant transpiration. In the absence of a better method for describing weather conditions, it may be stated that the temperature varied within the limits 30–35° C., and the sky was not without haze, though clouds were rare. We have considered nothing weaker than strong diffuse light, that obtained under a screen of tent canvas. The plant stomata were probably always in the day condition throughout these experiments, and incipient wilting, if it occurred, was probably not generally a controlling factor in the transpiration rates.

Several different shade intensities were included in the tests, but an inspection of the tables will convince one that the fluctuations in the correction coefficients do not appear to be related to any particular shade. In the following derivation of conclusions all tests will be considered as tentatively equivalent, and no attempt to weight the averages will be made. The coefficients of correction will be treated as the main criterion for judging of the relative degrees of sensitiveness of the plants and instruments toward variations in light intensity.

1. Considering all coefficients (tables III, V, and VI, not the averages) with values between 0.90 and 1.10, inclusive, as equal to unity, we see that *all* of those greater than unity have reference to the porous cup atmometers. The other instruments *always* recorded greater differences between the two light intensities than did any of the plants. To study the distribution of the different forms of coefficient more in detail we may proceed to classify them in each of these two groups of instruments. The frequencies of occurrence of coefficients less than, equal to, and greater than unity, for the three atmometers and the three plants, are presented in table VIII. For example, there are six coefficients greater than one occurring for the brown atmometer and *Physalis*, only one for

Xanthium, and none for *Martynia*. The last column of the table gives the total number of comparisons made.

TABLE VIII

Instrument	Plant	C 1	C=1	C 1	Total
Brown atm....	Physal.....	1	1	6	8
	Xanth.....	3	4	1	8
	Martyn.....	0	4	0	4
Black atm	Physal.....	2	1	5	8
	Xanth.....	3	4	1	8
	Martyn.....	2	2	0	4
White atm....	Physal.....	0	0	8	8
	Xanth.....	1	2	5	8
	Martyn.....	0	1	3	4

2. From table VIII we derive the generalization that for all cups, under all test conditions, *Physalis* shows the most frequent occurrence of coefficients greater than unity. *Martynia* shows the least frequent occurrence of these. *Physalis*, therefore, is usually more sensitive to light changes than the cups; the other two plants are generally equally sensitive or less so.

3. For the white cup, for all plants, and under all test conditions, the great majority (16 out of 20) of the coefficients are greater than unity. This cup is generally not as sensitive to light variations as are the plants.

4. The brown and black atmometers agree in giving mainly coefficients for *Physalis* which are greater than unity, while for the other plants they are equal to or less than unity; see 2.

Turning now to an analysis of the coefficients of the other instruments, we may treat them as we have the atmometers, only classifying them as less than, equal to, or greater than 0.50 instead of 1.00. We may consider as equal to 0.50 all coefficients from 0.40 to 0.60, inclusive. Table IX presents the classification on this basis.

5. It appears from this array of figures that the integrator gives predominance to coefficients greater than 0.50, while the other instruments give them equal to or less than 0.50.

6. "Solio" paper shows the strongest tendency to give coeffi-

cients less than 0.50, but half of those derived from this instrument are equal to 0.50.

TABLE IX

Instrument	Plant	C<0.50	C=0.50	C>0.50	Total
Integrator	Physal.	0	1	3	4
	Xanth.	1	1	2	4
	Martyn.	1	1	2	4
"Solio" paper	Physal.	2	2	0	4
	Xanth.	2	2	0	4
	Martyn.	2	2	0	4
Wynne paper	Physal.	0	4	0	4
	Xanth.	1	3	0	4
	Martyn.	2	2	0	4
Black therm	Physal.	0	3	1	4
	Xanth.	1	3	0	4
	Martyn.	2	2	0	4

7. From the Hicks integrator and the black bulb thermometer evidence is again presented that *Physalis* is more sensitive to light changes than either of the other plants, and it is suggested that *Martynia* may be somewhat less sensitive than *Xanthium*.

From the grand averages of table VII we may derive some approximate notion of the values to be taken, in general, as correction constants in the operation of these instruments. It must be borne in mind that the data are inadequate and the conclusions tentative in the extreme.

8. *Physalis* appears to be about a third more sensitive than the two dark cups, which agree well together. *Xanthium* and *Martynia* appear nearly to equal these cups in sensitiveness. The average correction factor for all three plants is 1.075.

9. *Physalis* appears to be about 60 per cent, the other two plants only about 25 per cent, more sensitive than the white cup. The average correction factor for the white cup is 1.36.

10. All three plants are somewhat more than half as sensitive as the Hicks solar radio-integrator, the average correction for which is 0.59; see 5 above.

11. The Wynne actinometer and the black thermometer agree well in showing a sensitiveness about double that of the plants,

more than double for *Physalis* and less than double for the others.

12. The Clements instrument, with "solio" paper, seems to be generally about three times as sensitive as are these plants, somewhat more than this for *Xanthium* and *Martynia*, somewhat less for *Physalis*. From these averages it appears more sensitive than by the method of frequencies; see 6 above.

On the whole, we may conclude that the black and brown atmometers and the Hicks integrator have shown themselves to be valuable instruments for estimating the solar intensity, so far as transpiration is concerned. They should be suitable for the comparison of light intensities in different habitats, etc., and they are especially to be recommended on account of their power of automatic integration, and also on account of the fact that they all give their results in terms of vaporization of a liquid, thus resembling the plant in its transpiration activity. The black bulb thermometer recommends itself as the best of the non-integrating devices. The photographic papers are not to be highly recommended as used in this inquiry, mainly on account of their failure to record effects of other than restricted wave-lengths. They may be modified so as to be more available, and may, possibly in their present form, be even more valuable than the other instruments here tested, when the effects of light variations on *photosynthesis* rather than transpiration are to be determined.

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THE EMBRYO SAC OF EPIPACTIS[1]

WILLIAM H. BROWN AND LESTER W. SHARP

(WITH PLATE X)

The present study is based upon material of *Epipactis pubescens* (Willd.) A. A. Eaton, collected at Cold Spring Harbor, N.Y., in August 1909.

The archesporium is distinguishable very early as a single hypodermal cell which terminates an axial row surrounded by a single epidermal layer. As growth proceeds, the young ovule becomes strongly anatropous and develops two integuments, the outer one being continuous with the slender stalk. Since the normal heterotypic prophases always occur in the nucleus of the archesporial cell preparatory to its first division, it is to be regarded as the megaspore mother cell, no parietals being formed.

The subsequent course of development to the complete embryo sac is not identical in all ovules, the same end being reached by a variety of methods. The behavior in what probably represent the majority of cases is as follows. After becoming considerably enlarged, the megaspore mother cell undergoes its first division (fig. 1). Since the spindle lies near the micropylar end of the mother cell, the resulting daughter cells are very unequal in size (fig. 2). The larger, chalazal cell again divides unequally, forming two megaspores, while in only a single case was the micropylar daughter cell observed in process of division (figs. 3 and 4). The innermost megaspore enlarges and gives rise to the embryo sac, while the other cells of the row soon degenerate.

The nucleus of the functioning megaspore divides to two (fig. 5), and very soon small vacuoles appear in the cytoplasm, mostly in the region between the two nuclei. Meanwhile the sac grows considerably, but continues to have the general shape of the megaspore mother cell. As growth proceeds, the increase in volume of the cytoplasm fails to keep pace with that of the sac cavity, so that

[1] Contribution from the Botanical Laboratory of the Johns Hopkins University No. 19. The account of the development of the embryo sac was written by Mr. SHARP, and the discussion by Mr. BROWN.

the small vacuoles in the central region coalesce to form a large central one (fig. 6), the cytoplasm becoming spread out as a parietal layer which is thickest at the ends of the sac where the radius of curvature is small. The two nuclei lie in these two regions. These nuclei soon divide simultaneously, giving rise to the four-nucleate sac (fig. 7). In this division and in the preceding one no traces of cell plates could be distinguished on the spindle fibers. After considerable enlargement of the embryo sac, the third division occurs, the two spindles formed in each end varying in position. Usually they lie approximately at right angles to each other; in such cases they may be equidistant from the end of the sac (fig. 8), or one may lie at a little distance from the other along the lateral wall. Cell plates appear on the fibers of all four spindles, so that the resulting eight nuclei are separated in the usual manner. In the micropylar end the transverse spindle gives rise to the two synergids, while the longitudinal one forms the egg and polar nucleus. In the chalazal end three antipodal cells and a polar nucleus are formed in an exactly similar manner (fig. 9). The egg and synergids increase in size, and the two polar nuclei approach each other and fuse (fig. 10).

Exceptionally the two spindles in the chalazal end of the sac, instead of lying at right angles, come to lie more or less parallel to each other and usually to the longitudinal axis of the sac (fig. 11). As division proceeds they may become coalesced, forming one large spindle instead of two ordinary ones (figs. 12–14). The conclusion that such is the explanation of the large spindle shown in fig. 12 is supported by the fact that the plate of chromosomes could be seen by focusing to be made up of two groups of approximately equal size, and that altogether their number was plainly larger than that in either of the micropylar spindles. The same was true of the corresponding spindle of fig. 13. The division of this double spindle may keep pace with that of the micropylar ones (fig. 12), or it may be delayed as shown by figs. 13 and 14. In fig. 14 the wall on the fibers of the chalazal spindle is only slightly younger than those of the micropylar ones, showing but a slight delay. In fig. 13 the delay has been greater, the chromosomes of the chalazal spindle having very recently separated, while in the micro-

pylar end distinct walls and nuclear membranes are present. The wall which appears on the fibers of the double spindle cuts off one nucleus in the base of the sac, and leaves one free in the cytoplasm (fig. 15). In these cases the latter nucleus apparently fuses with the polar nucleus from the typical micropylar group, while the one cut off by the wall later disorganizes (fig. 16). That such a six-nucleate condition offers no hindrance to fertilization is evidenced by the sac represented in fig. 16, in which a two-celled embryo is present.

In fig. 11 the chalazal spindles have taken up a nearly parallel position, but at too late a stage to coalesce, since membranes are already present about the four nuclei. It is probable that in this case a continuous wall would be formed across the base of the sac, cutting off two nuclei and leaving two free in the cytoplasm, but no sac was observed in which such an end had been reached. These phenomena appear in most cases to be in some way associated with a narrow configuration of the chalazal end of the sac at this time, and a consequent diminution in the amount of cytoplasm present there.

In other cases the fate of the megaspore mother cell is quite different from that described in the foregoing account. After enlarging somewhat the nucleus divides, the spindle lying at about the center of the cell, so that the thin wall formed upon the fibers separates the mother cell into two nearly equal daughter cells (fig. 17). The wall, however, soon disappears, leaving the two nuclei in a single cell cavity which is to form the embryo sac. Between the nuclei vacuolation occurs, so that the center of the sac comes to be occupied by a single large vacuole, the two nuclei taking up positions at opposite ends of the sac, where the greater part of the cytoplasm lies (fig. 18). Aside from the conspicuously larger size of the sac and its nuclei, this stage is closely similar to the corresponding one of a sac derived from a single megaspore. It is important to note that here the epidermal layer of the nucellus could be seen to be everywhere in contact with the sac, degenerating cells being clearly absent (cf. figs. 6 and 18).

The two nuclei again divide, and delicate walls appear on the spindle fibers between each pair of resulting nuclei. Later both

walls may become quite distinct (fig. 19), though they vary somewhat in position owing to the various planes in which the spindles may lie. In the figure shown they are transverse to the longitudinal axis of the sac, so that the four nuclei have a linear arrangement. Usually, though not always, these walls disappear very soon. In the event of their complete disappearance, there results a four-nucleate sac like that represented in fig. 20, which is essentially the same as one derived from a single megaspore, but is conspicuously larger. That the four nuclei here shown have resulted from fewer divisions from the nucleus of the archesporial cell than have those in four-nucleate sacs derived from one megaspore seems to be indicated by their relatively larger size (cf. figs. 7 and 20). A similar condition was pointed out in connection with the two-nucleate stage (cf. figs. 6 and 18).

At a stage as late as the four-nucleate sac it becomes very difficult to determine whether degenerating cells at the micropylar end of the sac are present or not, so that it is unsafe to depend too strongly upon them as a criterion, but after the examination of a large number of cases the present writers hold the view that the four nuclei, which, on account of their origin and the appearance of walls at the mitoses which give rise to them, are megaspore nuclei, and that these by one further division give rise to an eight-nucleate sac entirely similar to one derived from a single megaspore.

Important evidence in this connection is afforded by the wall formed between the two chalazal (megaspore) nuclei, which often shows a tendency to persist. In fig. 21 it is still visible as a remnant during the division to form the eight nuclei of the sac, the four spindles in this case showing an unusual irregularity in distribution. Since one of the micropylar spindles was in an adjacent section, it was not possible to demonstrate the presence of a wall in that end. In other cases the wall persists for a longer time, giving rise to the condition shown in fig. 22. Here it is observed separating the two undivided chalazal nuclei, while at the micropylar end the next division has taken place, cell plates being evident on the spindle fibers. A somewhat later stage is represented in fig. 23. The persistence of the wall seems to result in a delay of the nuclear divisions (fig. 21), or in their suppression, as shown by figs. 22 and 23.

The fact that in these cases the wall between the two chalazal nuclei is decidedly thicker than those between the micropylar nuclei would seem to indicate that it had been formed at the time of megaspore formation rather than later by a double spindle as described above, for in the latter case the division of the double spindle lags behind that of the micropylar ones. It thus appears that a six-nucleate sac of this type may originate by either of two methods.

Should the wall formed at the first division of the megaspore mother cell persist until after the second division, we should have a development similar to that of *Smilacina* (McAllister 9), in which the walls separating the four megaspores break down, leaving in a single large cell the four nuclei, which then divide once to form an eight-nucleate sac.

A number of two-nucleate sacs were observed with apparently but one degenerating cell present at the micropylar end. Further evidence on this point was not obtained, but these may represent cases in which the embryo sac is being derived from a daughter cell, or, in the light of the above, from two megaspores.

The development of embryo sacs from two or from four megaspores in a plant, which also forms them from one megaspore in the usual manner, may be regarded as steps in the reduction of the number of nuclear divisions occurring between the archesporial cell and the formation of the egg. When four megaspores take part in the formation of an eight-nucleate sac, the egg is removed from the archesporial cell by three divisions, as is also the case in *Cypripedium* (Pace 11), in which the egg nucleus is one of four formed in one daughter cell. Should one more division in any way be eliminated, the egg nucleus then being one of the four products of the reducing divisions, the gametophytic generation would be represented by a single nucleus, and the condition would be exactly comparable to that of the animal egg.

The further fate of the embryo sac, whether derived from one, two, or four megaspores, is apparently the same. The pollen tube makes its way through the micropyle into the sac, disorganizing one of the synergids, and liberates two male nuclei, one of which fuses with that of the egg, and the other with the product

of the fusion of the polar nuclei (fig. 24). The endosperm nucleus which results from this fusion enlarges but does not divide, and soon degenerates along with the antipodals (fig. 25).

The first division of the fertilized egg is transverse (fig. 16). The second division is in the micropylar cell and is also transverse, while the third (fig. 25) separates the chalazal cell into two by a longitudinal wall. These two divisions frequently occur simultaneously. Intermediate stages in the development of the embryo were not observed, but in the mature seed, which is of the usual orchidaceous type, it consists of a small, oval, undifferentiated mass of cells with no suspensor.

Discussion

Owing to the definite course of development in many of the animal eggs, the zoologists have been able to study some of the factors concerned. They have found in some cases that structures develop independently. In others some organs do not appear if certain parts are wanting, while in still other cases, as the lens of the amphibian eye (SPEMANN **14**), structures, which at one time probably required the presence of another organ for their development, have during the course of evolution come to develop independently.

The factors concerned in the development of plants have been studied much less than in the case of animals. This is perhaps due to the fact that most of the plants which show determinate development are inclosed, during their early stages, in the tissues of the parent. It is well known, however, that the form of a plant may be greatly affected by external conditions. A striking case is that of *Stigeoclonium*, in which, according to LIVINGSTON (**8**), the cells develop into a palmella stage or elongated filaments according to the osmotic strength of the nutrient solution. HARPER (**6**) in studying *Hydrodictyon* concluded that the shape of the net was due to the shape of the parent cell, while the axis of elongation of the individual cells was connected with the pressure exerted by neighboring cells upon each other.

In *Epipactis* it is not evident why the nucleus of a megaspore should in some cases develop into the nuclei of a whole embryo sac,

and in others into those of only a portion of one. This may be due, however, to some condition such as nutrition, which is external to the megaspores, and is probably not due to potentialities inherent in the various megaspore nuclei, for it would seem that the nucleus of each megaspore, if placed under proper conditions, would have the potentialities for producing the nuclei of a complete sac. This conclusion is supported by the large number of cases in which the development of more than one megaspore in a tetrad has been described (COULTER and CHAMBERLAIN **4**). Differences in the potentialities of the megaspore nuclei, moreover, could not explain the differences in development, for the course can be predicted at metaphase of the reducing division. Different potentialities if they existed would, therefore, have to be in the nuclei of the different megaspore mother cells; but according to present theories of heredity all mother-cell nuclei possess equal potentialities. The most reasonable conclusion would seem to be that the different courses of development are due to conditions external to the nuclei, and that the fate of a nucleus will depend on its position. It would seem probable, moreover, that the conditions which determine the fate of a nucleus, when four megaspores combine to form a normal sac, must be the same as those which determine the fate of the nuclei of a sac formed from a single megaspore. The formation of a normal sac from four megaspores in *Lilium* (COULTER and CHAMBERLAIN **4**), *Smilacina* (MCALLISTER **9**), and also in the large number of cases in which a row of megaspores is not formed, as well as from the aposporous outgrowths into the cavity of the degenerated embryo sac of *Hieracium* (ROSENBERG **13**), and in *Alchemilla* (MURBECK **10**) from the megaspore mother cell without a reduction in the number of chromosomes, would seem to indicate that the formation of a sac is not due to the nature of the cell from which it is produced, but that a normal sac will be formed from any cell subjected to the conditions under which a megaspore would produce one. The determining conditions in all of these cases, or at least most of them, are probably the same as in *Epipactis*, and since these conditions appear to be widely distributed among the angiosperms, they may have been the original cause of the evolution of the eight-nucleate sac. This could be true even

if it should be shown that some normal sacs are formed without the original determining condition, for cases apparently quite similar to this are known among animals. A striking example is the lens of the amphibian eye (SPEMANN 14), which in some species requires the presence of the optic cup for its development, while in others it develops even if the optic cup is removed.

From the foregoing discussion it does not follow that the nuclei play a passive part in development; for the external conditions which influence them may in turn be due to the nuclei from which these have been derived, i.e., the vegetative nuclei of the plant; and if a nucleus were other than it is, it probably could not react to external conditions to produce the structures which it does.

Any analysis of the conditions determining the course of development of the embryo sac must at present be incomplete and largely tentative, but a comparison of the conditions under which various types of sacs are formed may be worth while, as it is likely to suggest new ways of looking at their origin and development. The first point to be considered is the production of polarity. Before the megaspore mother cell divides, it has the general shape of the mature sac, and an enlargement of the whole nucellus without further change would preserve this shape. The formation of the megaspores in rows in most angiosperms, and the elongation of the nucellar cells in a direction parallel to this row would indicate that the elongated shape of the functional megaspore and the sac is connected with the direction of greatest pressure in the nucellus. When the nucleus of the mother cell divides, the daughter nuclei, as is usually the case, tend to be evenly distributed in the cytoplasm. After vacuolization, a continuation of this same tendency would carry the nuclei to the two ends of the sac, where surface tension would cause the accumulation of the cytoplasm. The conclusion that this is the explanation of polarity is supported by the development of the sixteen-nucleate sacs. In *Peperomia sintenesii* (BROWN 1), where the sac would seem to be derived from four megaspores, the mother cell and embryo sac are both rounded, and there is no polarity. The same thing is true in the Penaeaceae, where Miss STEPHENS (15) believes that the embryo sac is derived

from four megaspores. In *Peperomia hispidula* (JOHNSON **7**) and in *Gunnera* (ERNST **5**) the embryo sac is rounded at the four-nucleate stage and there is no polarity, but as development proceeds the sac elongates and polarity is produced. In *Strelitzia* (BROWN **3**) there are four megaspores, each of which may germinate, but the three micropylar ones degenerate and the sac is always formed from the chalazal one. The three micropylar megaspores are not elongated and their nuclei do not show a polar arrangement.

At the second division of the embryo sac of *Epipactis* the spindles are arranged so that the daughter nuclei are again evenly distributed in the cytoplasm.

At the third division the spindles in both ends are usually arranged approximately at right angles to each other. This is of course usually the case in the ends of embryo sacs and in other rounded masses of cytoplasm, and would seem to be the way in which the spindles and resulting nuclei would be most evenly distributed. In *Epipactis*, however, the chalazal end is sometimes narrow, and in this case the two spindles lie side by side. The simultaneous division of the nuclei and the production of an equal number in each end is probably connected with the similar conditions in the two ends. The number of nuclei is very likely due to some kern-plasma relation. In later stages the similarity of the two ends is destroyed and the nuclei take on quite different appearances. In *Epipactis* there is sometimes less cytoplasm in the chalazal than in the micropylar end, and this is connected with a delay in the divisions in the chalazal end.

STRASBURGER (**16**) has pointed out that the walls produced at the last division in a normal eight-nucleate sac are formed on the fibers connecting the nuclei, and that since one nucleus at each end is nearer the center than the other three, no wall is formed around it, thus leaving it free in the cytoplasm. He ascribes the fusion of these two polar nuclei to the fact that they have ceased developing and are in the same cell cavity. Evidence strengthening this position has been constantly accumulating and, as previously pointed out (BROWN **1**), is quite striking in the case of the sixteen-nucleate sacs, where all of the nuclei not cut off by walls fuse to form the endosperm nucleus. In *Epipactis* the polar nuclei are

produced in a variety of ways, but always fuse to form the endosperm nucleus, although this does not develop further.

It would seem that even the final fate of the nuclei may depend largely on interacting conditions, for the synergids in those cases in which a sac is formed from four megaspores, as in the normal cases, are formed from the pair of nuclei arising from the transverse spindle. That the nuclei at this stage are equipotential is indicated by the occasional fertilization of one of the synergids (COULTER and CHAMBERLAIN 4). The structure of eggs, synergids, antipodals, etc., probably depends largely on the nature of the protoplasm of which they are constituted, and is of course widely different in different plants; but the part which any particular nucleus in *Epipactis*, and probably in other angiosperms, is to produce, as well as the general arrangement of the sac, apparently depends on the relation of the nucleus to other parts rather than upon any quality inherent in it.

According to the above interpretation, the embryo sac in its early stages may be regarded as a system, all parts of which are equipotential, the fate of the different parts being connected with conditions external to them. The course of development in certain animal eggs is connected very largely with a stratification of the materials composing them, but in the early stages of many of these eggs a cell may develop into a whole embryo or some fraction of one, depending on whether or not it is separated from others. This dependence of the course of development of a cell on its relation to conditions external to it, therefore, seems to be common to both plants and animals.

The foregoing analysis, in so far as it goes, may be taken as indicating that the parts concerned act according to mechanical principles and do not need a vitalistic force to explain their behavior. This would seem to be true of any analysis which shows an orderly relation between an antecedent and consequent event, because for a thing to be mechanistic (this term being used in its widest sense) means simply that when the events are reduced to their simplest terms they take place in an orderly and predictable sequence. An analysis may bring to light new elemental laws of a different

kind from any that we know at present, but in so far as they are laws of an orderly sequence, they will be as good a mechanical explanation as any other law, for a law can only state the sequence, and it is outside the realm of science to explain why one event follows another. Any vitalistic explanation must therefore be either outside and supplementary to science or contrary to the fundamental postulate of all science, namely, that the same antecedent conditions are always followed by the same consequent ones.

If we compare the development of the angiosperm embryo sac with that of the gymnosperms, we find in the early stages a striking similarity between those of the gymnosperms and the sixteen-nucleate sacs of the angiosperms. In both cases the nuclei are fairly numerous, evenly distributed in the cytoplasm, and do not show a polar arrangement. This similarity, however, is probably derived and not primitive in the case of the sixteen-nucleate sacs, for some of these, at least, are derived from four megaspores. There would appear to be in the gymnosperm embryo sac nothing similar to the striking polarity shown by those of most angiosperms, but that the same factors are at work is perhaps indicated by the elongated shape of the embryo sacs of many of the gymnosperms, as well as the tendency toward a reduction in the number of nuclei, and the presence of a large central vacuole. Likewise the presence in the early stages of the gymnosperm embryo sac of free nuclei surrounded by a cellular region may foreshadow the free polar nuclei of the angiosperms. PORSCH (**12**), in an excellent discussion of the phylogeny of the angiosperm embryo sac, has attempted to point out a similarity between the archegonia of the gymnosperms and the two polar groups in the angiosperms. When we remember, however, that in those gymnosperms which have archegonia they are initiated in a cellular phase and the polar groups of the angiosperms in a non-cellular one, it would seem that any similarity between the development, final structure, or factors concerned must be rather superficial. It would probably be better to regard the structure of the angiosperm embryo sac as the result of new physiological conditions which have arisen in connection with the reduction of its size and the number of its nuclei.

Summary

1. The archesporium of *Epipactis* consists of a single hypodermal cell, which, without formation of parietals, functions as the megaspore mother cell.

2. In most cases the megaspore mother cell divides to two unequal daughter cells, the chalazal one again dividing to form two megaspores. The innermost megaspore then gives rise to the embryo sac.

3. In other cases four megaspores take part in the formation of the sac, the walls appearing at the first two divisions of the megaspore mother cell being evanescent. At least one of these walls often shows a tendency to persist, which results in a six-nucleate type of sac. The same appearance may also result from irregularities in the orientation of spindles.

4. There is some evidence that the embryo sac may at times be derived from two megaspores.

5. The normal mature embryo sac contains an egg, two synergids, three evanescent antipodal cells, and two polar nuclei which fuse.

6. The usual type of "double fertilization" occurs.

7. The fertilized egg gives rise to an embryo, which, at least in the seed, has no suspensor.

8. The endosperm nucleus, formed by the fusion of one male nucleus with the two polar nuclei, disorganizes without dividing.

9. The variety of methods by which the embryo sac of *Epipactis* is formed may be regarded as a series representing a reduction in the number of nuclear divisions occurring between the archesporial cell and the formation of the egg.

10. The fate of the nuclei in the different courses of development is probably due to some conditions external to them rather than to any inherent potentialities. A normal sac would probably be produced by any cell subjected to the conditions under which a mother cell would produce one.

11. The sac in its early stages appears to be an equipotential system, polarity being connected with its shape, and the part that the nuclei are to play with their position.

12. The polar groups probably do not represent archegonia,

but the general structure of the angiosperm embryo sac may be indicated by some features in those of the gymnosperms.

The writers wish to express their thanks to Professor C. B. DAVENPORT, director of the biological Laboratory of the Brooklyn Institute of Arts and Sciences, for courtesies shown them during their stay at Cold Spring Harbor; and to Professor D. S. JOHNSON for helpful suggestions and criticisms during the progress of the work.

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EXPLANATION OF PLATE X

All figures were drawn with the aid of an Abbé camera lucida, and show a magnification of 900 diameters. The following abbreviations are used: *a*, antipodals; *d*, daughter cell of megaspore mother cell; *e*, endosperm nucleus; *m*, megaspore; *pt*, pollen tube; *s*, synergid; ♂, male nucleus.

FIG. 1.—First division in the megaspore mother cell.

FIG. 2.—Daughter cells resulting from division of megaspore mother cell.

FIG. 3.—Two megaspores formed by the division of the chalazal daughter cell, and the undivided micropylar daughter cell.

FIG. 4.—Micropylar daughter cell dividing; the only case observed.

FIG. 5.—Young two-nucleate sac; spindle fibers still present; no separating wall; abortive megaspore and daughter cell represented by two deeply staining masses.

FIG. 6.—Two-nucleate sac after formation of central vacuole.

FIG. 7.—Four-nucleate sac.

FIG. 8.—Division to form eight nuclei.

FIG. 9.—Eight-nucleate sac.

FIG. 10.—Fusion of polar nuclei.

FIG. 11.—Division to form eight nuclei; the two chalazal spindles show a tendency to become parallel to each other.

FIG. 12.—Metaphase of a similar division; the two chalazal spindles have coalesced to form a single large spindle.

FIG. 13.—Later stage; the division of the coalesced chalazal spindles lagging behind that of the micropylar ones.

FIG. 14.—Telophase of a similar division; wall appearing on the fibers of the spindle formed by coalescence.

FIG. 15.—Wall complete; the nucleus cut off in the base of the sac beginning to disorganize; its sister nucleus free in the cytoplasm with the polar nucleus of the micropylar group.

FIG. 16.—Sac containing two-celled proembryo, endosperm nucleus, disorganized cell in base, and pollen tube.

FIG. 17.—Nearly equal division of megaspore mother cell; wall formed on the spindle fibers.

FIG. 18.—Later stage; the wall has disappeared and a central vacuole has formed.

FIG. 19.—Four megaspore nuclei with evanescent walls.

FIG. 20.—Four megaspore nuclei; the walls have disappeared.

FIG. 21.—Four megaspore nuclei dividing to form the eight nuclei of the sac; megaspore wall still evident in chalazal end.

FIG. 22.—Sac in which the chalazal megaspore wall has persisted.

FIG. 23.—Later stage; walls in micropylar end complete.

FIG. 24.—Double fertilization in a typical eight-nucleate sac.

FIG. 25.—Sac containing young embryo; endosperm and antipodal nuclei disorganizing.

BROWN and SHARP on EPIPACTIS

THE OXYGEN MINIMUM AND THE GERMINATION OF XANTHIUM SEEDS

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 152

CHARLES ALBERT SHULL

(WITH ONE FIGURE)

Although delayed germination has received considerable attention during the last few years from investigators both in America and Europe, not much has been accomplished toward solving the problems presented by this phenomenon. This may be due in large measure to lack of exact, or at least quantitative, methods of investigation, and to mental attitude which may modify the interpretation of results. Vitalistic interpretations of phenomena may at times prevent a close analysis of the physical and chemical phenomena which condition the manifestations of life, thus preventing the solution of the real problems.

During the last two years the writer has been engaged in an investigation of the relation of oxygen pressure to the germination of *Xanthium* seeds. The need of oxygen for germination and growth of organs in the higher plants has been under discussion for some time. TAKAHASHI (**27**) has shown that rice can germinate in complete absence of free oxygen, and CROCKER (**5**) has shown the same to be true for the seeds of certain water plants, as *Eichhornia* and *Alisma Plantago-aquatica*. NABOKICH (**20**) has experimented on the hypocotyls of *Helianthus annuus*, *Vicia Faba*, and *Phaseolus vulgaris*, and concludes that the organs of higher plants generally are able to grow in entire absence of oxygen. A rather small number of species was used from which to draw sweeping conclusions. LEHMANN (**18**) investigated the anaerobic growth of the organs of higher plants, and found that there is practically no growth in epicotyls at 1 or 2 mm. of atmospheric pressure. In some instances, as with *Helianthus annuus*, growth of the hypocotyl occurred in total absence of oxygen in distilled water at a temperature above 25°. In 0.5–1 per cent sugar solution, growth occurred even at 20°, but was slight. A number of plants, *Vicia Faba*,

Pisum sativum, *Brassica Napus*, *Lupinus albus*, and *Cucurbita*, failed to grow in total absence of oxygen, either in water or in sugar solution, at any temperature. It is evident that the organs of higher plants vary according to species in their need of oxygen for growth and germination.

The results obtained with *Xanthium* seeds emphasize this variability, as will be shown later. A preliminary report of this work (**26**) was published some time ago, since which time the work there outlined has been largely completed. The problem was suggested by Dr. WILLIAM CROCKER, and has been pursued under his direction at the Hull Botanical Laboratory. It is a pleasure to acknowledge my indebtedness to him for many helpful suggestions during the course of the experiments, and for making during my absence from the University of Chicago some accurate determinations of the vapor pressure present in the apparatus under experimental conditions.

Historical

The literature on delayed germination has been reviewed so recently by others that a detailed account of the earlier work is not necessary here. Some of the earliest experiments were carried on by NOBBE (**21**) during the decade 1870–1880, in connection with the testing of agricultural seeds. A little later NOBBE and HÄNLEIN (**22**) tested many weed seeds, obtaining remarkable results; and finally HÄNLEIN (**11**) reported on a large number of seeds which he kept in germinative conditions for 1173 days, many of which showed a fraction of 1 per cent of germination, while of *Phyteuma spicatum* L. and *Primula elatior* Jacq. not a single seed germinated in that time. These investigators recognized that the testa in some cases excluded water and prevented germination. But when the testa allowed water to enter, which was not infrequent, and still no germination occurred, both writers refer to this phenomenon as an inexplicable "Rätsel."

HÄNLEIN recognized another category of behavior, however, in which the resistance of the seed to germinative conditions is not external and mechanical, but is internal and protoplasmic. The character of the ovule, the origin, character, and age of the fertiliz-

ing pollen, the nutrition of the parent plant, accidents of sun and shade, moisture and dryness of soil, high and low altitude, weather conditions during ripening, the time of harvesting, and subsequent handling of seeds are suggested as influential factors in determining germination behavior.

The germination of *Xanthium* seeds was first investigated by ARTHUR (1), who noted the dimorphic character of the two seeds in the bur, and found that the lower seed germinated in the spring after ripening, while the upper seed germinated the second year or later. Believing that the testa was too nearly alike in both seeds to cause this difference, and finding much more reducing sugar in the lower seed than in the upper after exposure to germinative conditions, he suggested that enzymes were produced in the lower seeds more readily than in the upper, and that the delayed nutrition of the embryo of the upper seed was the probable cause of the delay in germination.

MASTERMAN (19) tested the germination of *Xanthium* in some field experiments during several years, and showed that over 90 per cent of the burs grew both seeds the same year, thus contradicting the statement of ARTHUR that the upper seed was usually delayed till the second year or later. MASTERMAN'S experiments were not critical, but the results that he and ARTHUR obtained are readily explained and harmonized in the light of more recent investigation.

PAMMEL and LUMMIS (24) found that weed seeds germinated a much higher percentage of seeds after having been frozen than before. In the case of *X. canadense*, they found that none of the fresh seeds germinated during the fall, but after freezing and thawing during the winter, over 50 per cent of them germinated. FAWCETT (7) obtained similar results with many kinds of weed seeds, the percentage of germination being increased, and the "period of dormancy" shortened by freezing again and again.

If the upper cocklebur seed is delayed till the second spring or later, it is because it has resisted the forces of disintegration which finally make possible the entry of oxygen in sufficient quantity for germination, or has not experienced the high temperatures which CROCKER has shown will cause the germination of uppers with

coats intact. Such resistance may be the usual thing in seeds collected and kept at an even temperature during the first winter. But in nature the extremes of winter climate must often destroy the integrity of the coats of these seeds, thus admitting the oxygen necessary for growth. And even if the seed coat is intact, the high temperature often experienced during the spring and early summer is sufficient to germinate the upper seeds if they are near the surface of the ground, since temperatures between 30 and 35° C. cause germination of the uppers with coats intact. Thus it is seen that the results of ARTHUR and MASTERMAN may both be correct under proper circumstances, and the discrepancy in their results is readily accounted for.

Later CROCKER (4), in testing ARTHUR'S enzyme theory, discovered that the cause of delay in the upper seed lay in the seed coat, which, though not excluding water, restricted the supply of oxygen to the embryo to such an extent that growth was temporarily suppressed. He tested many other seeds which showed delayed germination and found that, contrary to the usual opinion, in the majority of cases the coat was responsible for the delay by exclusion or restriction of oxygen or water. He pointed out that the restriction of oxygen for the embryo by the testa gave these seeds an exceptionally high minimum temperature for germination, and that, since the seed coats of uppers and lowers differed in the degree of restriction, two minimum temperatures exist for each seed, one with the coat intact, the other with the coat removed. He suggested that high temperatures caused germination by hastening the diffusion of oxygen through the seed coats; but since it is shown in this paper that a rise of temperature decreases the amount of O_2 demanded for growth, the question as to the influence of temperature on diffusion in this particular case is an open one.

High oxygen pressures brought about germination in a short time, but not in the usual manner. The cotyledons elongate sooner than the radicle, due to the thinness of the testa at the distal end of the seed permitting the diffusion of oxygen more readily over the cotyledons.

CROCKER (5) tested seeds of water plants also, and showed that in many instances the delay in germination was due to coat char-

acters, which exclude or restrict the supply of water, rather than to embryonic characters.

At about the same time certain German investigators published a number of papers dealing with similar problems, which are of interest chiefly because of the interpretations of their results. CORRENS (**3**) found a higher percentage of germination in the disk seeds of *Dimorphotheca pluvialis* than in the ray seeds. He ascribed the difference in percentage of germination to the different constitution of the embryos, but CROCKER showed that in the dimorphic seeds of *Axyris amaranthoides* the non-winged seeds were delayed by coat characters, and that the percentage of germination did not differ when the coats were broken, both showing 100 per cent in three days.

ERNST (**6**), working with seeds of *Synedrella nodiflora*, showed that light of various intensities and refrangibility affected the length of time necessary for germination, and he attributed not only percentage of germination but also the length of time necessary for germination to the constitution of the embryo.

FISCHER'S (**8**) paper on the influence of hydrogen and hydroxyl ions on seeds of aquatic plants appeared shortly before CROCKER'S work on the seeds of the same plants. FISCHER interpreted his results as showing that the ions stimulated and awakened the supposedly dormant protoplasm to activity, and thus caused germination to occur. But as already intimated, it was shown by CROCKER that the protoplasm of the seeds of these aquatic plants is not dormant, and needs no stimulus except the necessary conditions for germination, which are supplied if the testa is removed or broken.

OSTENFELD (**23**) found that digestive enzymes of birds favored the germination of seeds, but he refrained from ascribing the results to the effect of the enzyme on the embryo, saying that the question raised by the widely different interpretations of FISCHER and CROCKER was an open one.

Following the work of ERNST mentioned above, KINZEL (**12–16**) has shown that light is a factor in the delayed germination of many seeds. The data accumulated show that in some way light of various intensities and refrangibility modifies the seed with the testa intact. The interpretation in all cases ascribes the results

to the protoplasmic characters of the embryo, which are supposed to be changed so that the seed becomes more active or less active by exposure to light. The uses of such terms as "lichtmüde" and "dunkelhart" as applied to protoplasm gives one the characteristic viewpoint.

Very recently GASSNER (**9, 10**) has studied the effect of light on the germination of some South American Gramineae. His interpretation is in harmony with that of KINZEL, the effect of the light being considered as exerted upon the embryo.

In none of these recent investigations have the methods been sufficiently refined to locate with certainty the cause of the delay. Before the real truth in regard to the cause of delay in many of these instances can be ascertained, more exact and analytical methods of procedure must be brought to bear upon the problem. A careful reinvestigation of some of these cases will not only probably locate the causes, but also reveal the nature of the causes of delay.

Materials and methods

This investigation of the germination of the seeds of *X. pennsylvanicum* and *X. glabratum* was undertaken after the discovery had been made that the oxygen pressure necessary for germination with testa removed was lower than the results CROCKER obtained with them intact would seem to indicate, and with the knowledge that the seeds of some higher plants, as *Alisma*, *Eichhornia*, rice, etc., could germinate in entire absence of free O_2. Seeds were collected in various places. Those used during the first season were secured in vacant lots in and near Chicago during the spring of 1909. One lot of seeds had been collected in the autumn as soon as ripe, and were kept in cool dry storage during the succeeding winter and spring. During the second season, seeds were used which had been collected in Lexington, Ky., in November 1909, and kept in an unheated dry room until June 1910. These seeds would all be included in Gray's *X. canadense* Mill., but BRITTON'S treatment of the genus is certainly more satisfactory than GRAY'S, and I use the names *X. pennsylvanicum* Wallr. and *X. glabratum* Britton as in the BRITTON *Manual*. I am indebted to Dr. J. M. GREENMAN for examining the seeds and

permitting me to see and compare my materials with the genus collection of *Xanthium* in the Field Museum of Natural History.

In determining the minimum oxygen pressure required for the initiation of protoplasmic activity, reduction of total atmosphere was employed. The apparatus used at first was a slightly modified form of that used by SCHAIBLE (**25**) in his experiments on the germination and growth of various plants at reduced atmospheric pressures. In order to control the light, the germinators were at

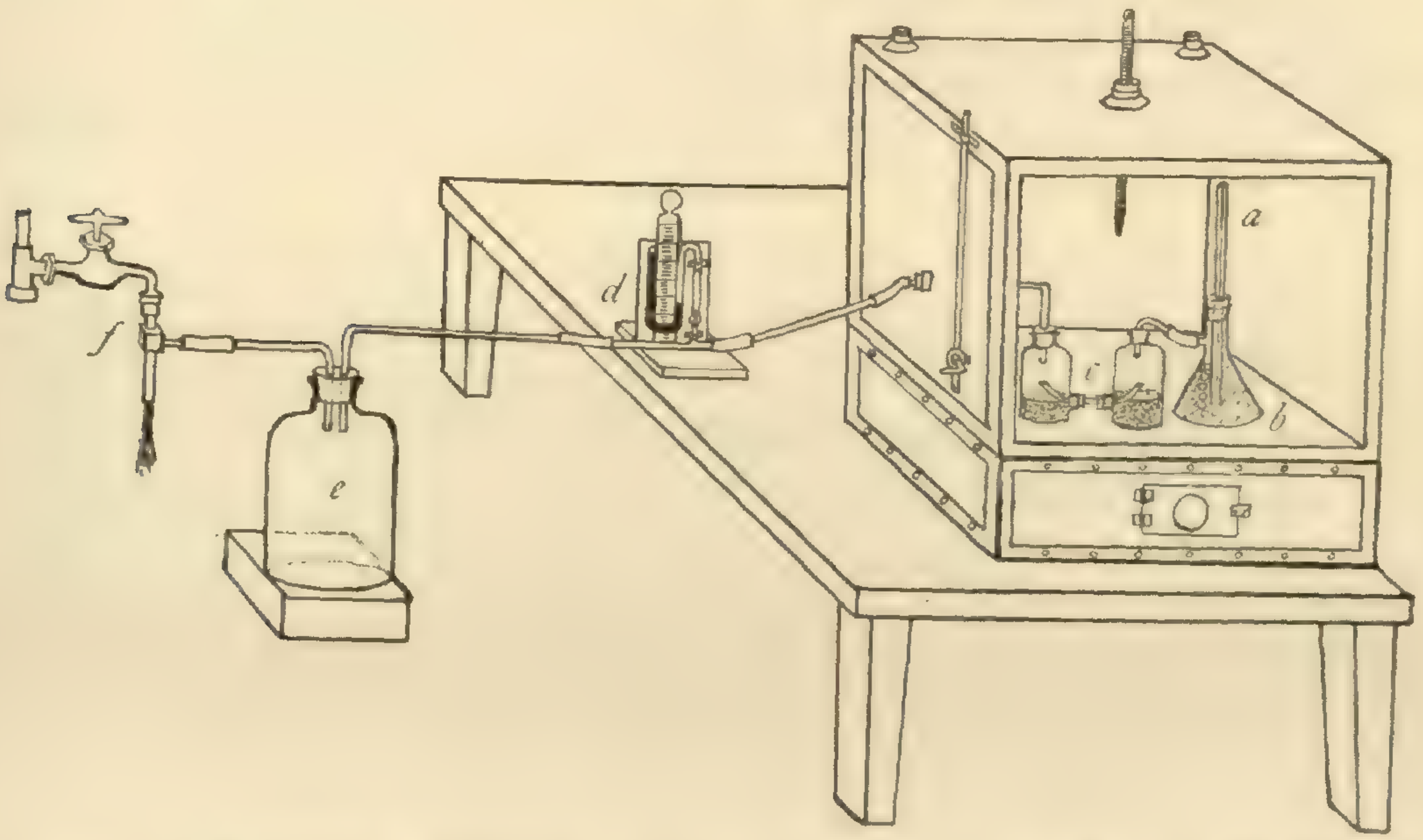

FIG. 1.—Diagram of apparatus: *a*, capillary tube; *b*, wash bottle; *c*, two germinators with wet cotton, for lowers and uppers; *d*, pressure gauge; *e*, vacuum chamber to secure immediate low pressure when the germinators are started; *f*, aspirator run by constant level system with a fall of 45 feet.

first surrounded by opaque black paper; but later, when temperature was found to be a very important factor in the result, and while testing the influence of temperature on the oxygen minimum, light and temperature were both controlled by placing the germinators in a water bath provided with a sensitive electric thermostat. A diagram of the apparatus is shown in fig. 1.

The seeds were germinated on moist absorbent cotton, and a constant current of air was drawn into the apparatus through long pieces of capillary tubing by means of powerful aspirators. In order to overcome the drying effects of a low atmosphere, a dish of water was set in each germinator in addition to the saturated

absorbent cotton on which the seeds lay. This method was discarded for the temperature and pressure experiments, as a more satisfactory arrangement consisted in immersing the lower end of the capillary tube in a flask of water, thus drawing the atmosphere through water before it entered the germinator. This method had the added advantage of showing at once whether the flow of air through the capillary tubes was being interfered with by dust particles. The air was kept moist in this way, but owing to the very rapid exchange of gas in the apparatus, the atmosphere was not saturated. The water which ran the aspirators had a fall of 45 feet, and was furnished through a separate constant level system which gave the aspirators uniform power.

The seeds were in all cases prepared for experimentation by soaking them in ice water, far below the minimum temperature for germination, for at least 12 hours, after which the testa was removed carefully, without injury to the seeds. They were exposed to constant conditions for 10 days, and the elongation of the hypocotyl and the geotropic response was used as the criterion of germination.

Temperature series at various pressures were run at 31° C., and the influence of fluctuating temperature was determined by using a fluctuation of 25–40° C.

At the low pressures and high temperatures employed, the evaporation of water in the apparatus is very rapid. In determining the actual oxygen pressures to which the seeds are subjected, it is necessary to know what volume of air is drawn through the apparatus in a given time, and what part of the gas pressure is due to water vapor. The atmosphere is not saturated, for if it were saturated at these reduced pressures, the water vapor pressure alone would be much higher than the total pressure used. The amount of air at normal pressure entering the apparatus is 3–5 liters per hour, a very rapid exchange, since it means 8–12 times that volume per hour within the germinators due to expansion under diminished pressure. Under such circumstances it is not surprising to find that the water vapor is removed so rapidly that the saturation point is not approached. It was clearly demonstrated, however, that water was not a limiting factor in these experiments.

Any increase of the aqueous vapor about the seeds was invariably attended by a marked decrease in the percentage of germination and amount of growth, due to the fact that such increase necessarily reduces the oxygen supply of the germinating seeds. In spite of the rapid evaporation and removal of the water, there is sufficient moisture present to bring about all the growth changes which the oxygen supply will permit, as was shown by repeated tests.

In correcting the pressures for water vapor, the only practicable method is to measure directly the amount of dry air passing into the apparatus per hour, and the amount of water vapor drawn from it in the same length of time, then calculate the proportion of each gas in the gram molecular volume. A concrete example will make the method clear. At 88 mm. pressure, 30° C., the dry air drawn through the apparatus measured at 20° C., barometer 745 mm., is 4.37 liters per hour. Reducing this volume to standard temperature and pressure gives 3.9 liters. This volume is 0.178 of the molar volume. The amount of water vapor present with that amount of air drawn from the apparatus as determined by phosphorus pentoxide absorption was 1.65 grams per hour; and this amount is readily found to be 0.086 of the molar volume. The dry air and water vapor together amount to 0.264 of a mole per hour. The pressure recorded by the manometer is 88 mm. Of this amount, 178/264 (59.3 mm.) is air pressure, 86/264 (28.7 mm.) aqueous pressure. The oxygen pressure is then readily obtained, as oxygen constitutes 20.93 per cent of the atmosphere. The corrections were made on the basis of the average of three determinations, and are therefore fairly reliable.

To determine whether reduction of pressure *per se* has any effect on germination, hydrogen gas with a low oxygen content was admitted to the chambers containing the seeds. The hydrogen was imported by the Linde Air Products Co., of Buffalo, N.Y., and was found to contain 2.34 to 4.7 per cent of oxygen. The gas with more than 2.5 per cent of oxygen was of little use, because the oxygen pressure was so high that no comparison with the reduced pressure experiments could be made. This hydrogen was under 120 atmospheres of pressure, but was controlled by high

pressure valves so that a small stream of gas at normal pressure ran constantly through the germinators.

The gas was washed by passing it successively through potash bulbs containing concentrated potassium permanganate solution, and 33 per cent potassium hydroxide. The whole series of coils and jars was packed in ice for 12 hours after the hydrogen began to flow, and the gas was carefully analyzed by phosphorus absorption until it was found to be coming from the apparatus with as low oxygen content as when taken directly from the tank, at which time the temperature was allowed to rise sufficiently for germination. In this way the possibility of the initiation of germination in only a partially replaced atmosphere was precluded. The apparatus was quickly brought to ordinary temperature, and kept constant at 21.5° C. by allowing a current of water from Lake Michigan to flow over and around the potash coils and germinators. Reduced atmosphere experiments at the same temperature were run at the same time, but the correction for water vapor in these series makes a direct comparison with the results in hydrogen impossible. However, comparison of these hydrogen results with other low pressure series run in the same way, makes it possible to draw trustworthy conclusions.

Attempts were made to test the after-ripening of *Xanthium* seeds of different ages, from green to a year old, at normal and reduced pressures. These experiments were not extensive, and on the whole not very satisfactory; but the results indicate that only very slight changes occur.

In all cases control cultures were employed. In measuring the growth of the controls, a difficulty presented itself. At full atmospheric pressure the roots of *Xanthium* seedlings penetrate the substratum of cotton with innumerable branches, impossible of disentanglement and accurate length measurement. In all these cases only the unbranched portion of the plant was measured. In all the experimental plants the total growth in length was easily measured and is so recorded.

Experiments

As indicated above, the experiments proceeded along four lines: to determine the minimum oxygen pressure necessary for germina-

tion, and to determine the influence of temperature, pressure, and after-ripening on that minimum. Since the first of these determinations is that on which the others bear, that portion of the work will be considered immediately.

THE MINIMUM OXYGEN PRESSURE

The tabulated results of these experiments are given in the preliminary report, but for convenience they are presented here again, with one addition, a test with *X. glabratum* (all others are *X. pennsylvanicum*) at 85 mm., and with correction of the oxygen pressure for aqueous vapor.

TABLE I

DURATION OF EXPERIMENTS 10 DAYS

MANOMETER PRESSURE (MM.)	AQUEOUS PRESSURE (MM.)	ATMOSPHERIC PRESSURE (MM.)	OXYGEN PRESSURE (MM.)	TEMPERATURE (C.)	PERCENTAGE GERMINATION				GROWTH IN LENGTH OF HYPOCOTYL (MM.)			
					Lowers	Controls	Uppers	Controls	Lowers	Controls	Uppers	Controls
99.....	16.4	82.6	17.3	19–22	75.0	100	45	95	14.5	30.0	4.9	23.3
90.....	16.3	73.7	15.4	21–22.6	80.0	95	50	100	22.8	45.9	4.3	37.8
85.....	16.25	68.75	14.39	21.5	56.6	93.3	23.3	100	42.8	103.64	10.5	94.9
72*....	16.14	55.86	11.69	20–28	45.0	100	20	100	11.5	46.0	9.4	33.6
72.....	16.14	55.86	11.69	20–22	30.0	95	0	100	6.36	28.5	0.0	22.0
28*....	15.27	12.73	2.66	21.5–24.5	0.0	100	0	95	0.0	37.8	0.0	28.8

* Temperature not controlled.

The table shows at once that there is a marked difference between the upper and lower seeds in percentage of germination and amount of growth under identical conditions, this difference being the expression of a decided difference in the oxygen need of the two seeds for germination. The difference in percentage of germination at each pressure and temperature used is fairly constant, the lowers germinating about 30 per cent more seeds than the uppers in each experiment. The difference in the oxygen need is several millimeters, the lowers requiring less oxygen than the uppers for the initiation of activity. The oxygen minimum for the uppers is approximately 12 mm., at 21° C., while the minimum for the lowers is about 9.5 mm.

It is important to notice the relation which this physiological difference in the embryos of the two seeds bears to the difference

in their seed coats. CROCKER found that restriction of the oxygen supply by the testa was the main cause of delay in germination, and that difference in the degree of exclusion by the testa of upper and lower seed accounted for the difference in delay of the two seeds. But this embryonic difference, which is clearly demonstrated in the table, acts in conjunction with the coat differences in securing a longer delay in the upper than in the lower seeds.

In comparison with the seeds and organs of other plants, the oxygen demand of *Xanthium* seeds is very high. As already noted, most seeds will germinate with not more than a few millimeters of atmosphere, and some germinate without free O_2, but *Xanthium* requires 9–12 mm. of oxygen, the equivalent of 44–60 mm. of atmosphere. This high demand for oxygen aids in securing delay, for if only a small fraction of a millimeter were needed for germination, the testas might not restrict the supply sufficiently to cause delay. And the difference in demand of the two seeds would secure a longer delay for the uppers than for the lowers, even if the testas did not differ in their power to exclude oxygen from the embryos as they do.

TEMPERATURE AND THE OXYGEN MINIMUM

It was found that temperature is a powerful factor in determining the oxygen minimum, slight changes producing marked effects upon the results. The potent influence of temperature in this regard is shown clearly by the two lots of seeds of *X. pennsylvanicum* kept at a pressure of 72 mm. as recorded in table I. The variation noted in these two lots was due to one lot being subjected to a temperature 6° higher than the other during a part of the last two days of the experiment. Previous to that time, the behavior of the two lots of seeds had been almost identical; but 45 per cent of the lowers germinated in the lot which reached 28°, as compared with 30 per cent, the lot which did not go above 22°; and 20 per cent of the uppers germinated as compared with complete failure to germinate at the lower temperature. The amount of growth in each lot shows a similar relationship.

In another instance shown in table I, two lots of seeds were subjected to atmospheric pressures of 90 and 99 mm. respectively,

but the latter lot was subjected to a temperature 2° lower on the average than the former. The results show, instead of an increase in percentage of germination and growth in length, as would have been expected from the increased supply of oxygen, a decrease of 5 per cent in the germination of both lowers and uppers, and a considerable decrease in the average growth of the lowers in length.

A number of experiments were performed with the purpose of determining how much effect temperature has on the location of the minimum. The results are presented here in tabular form. For the sake of comparison, one experiment at 72 mm. and room temperature is included at the bottom of the table, which may be compared with the results at 76 mm. and 31°, and with those at 75 mm. and 25–40°.

TABLE II

DURATION OF EXPERIMENTS 10 DAYS

MANOMETER PRESSURE (MM.)	VAPOR PRESSURE (MM.)	ATMOSPHERIC PRESSURE (MM.)	OXYGEN PRESSURE (MM.)	TEMPERATURE (C.)	PERCENTAGE OF GERMINATION				GROWTH IN LENGTH OF HYPOCOTYL (MM.)			
					Lowers	Controls	Uppers	Controls	Lowers	Controls	Uppers	Controls
76.....	29.0	47.0	9.8	31	93.3	100	40.0	100	50.4	102.0	32.75	109.0
65.....	29.1	35.9	7.5	31	60.0	100	43.3	100	33.1	102.0	20.15	109.0
65.....	29.1	35.9	7.5	31	80.0	100	10.0	100	32.4	79.6	24.00	86.6
55.....	28.7	26.3	5.5	31	66.6	100	0.0	100	11.6	79.6	0.00	86.6
75.....	Varies	with	temp.	25–40	93.3	90	56.6	100	37.25	67.4	28.00	70.6
65.....	Varies	with	temp.	25–40	86.6	90	26.6	100	32.9	67.4	17.25	70.6
72.....	16.4	55.86	11.69	20–22	30	95	0.0	100	6.36	28.5	0.0	22.0

The difference between uppers and lowers in percentage of germination is even more pronounced at 31° than at 21°, amounting in some instances to 60 or 70 per cent more germinations among the lowers than among the uppers. It appears also from table II that the oxygen minimum is considerably lower at 31° than at 21°, especially for the lower seeds. From the data here presented the oxygen minima have been approximated by mathematical methods. Since a pressure of 65 mm. germinated 10 per cent of the uppers, the oxygen minimum as calculated from the results would be about 6.75 mm. The minimum for the lowers was not accurately determined, but at 55 mm. atmospheric pressure, representing an O_2

pressure of 5.5 mm., there was still 66.6 per cent of germination. The closest estimation possible from the data at hand would indicate an oxygen minimum of about 2.5–3.5 mm. for the lowers at 31°.

The lowering of the minimum is somewhat greater in the lower than in the upper seeds. The oxygen minimum of the uppers is decreased from about 12 mm. to less than 7 mm., while for the lowers the minimum is decreased from 9.5 to about 3 mm. All of these results show that with the increase of temperature there is a decrease in the demand for free oxygen. The probable reason for this will be discussed later. The physiological difference of the embryos of the upper and lower seeds is shown clearly by these experiments, the embryo characters being just as strikingly different as the coat characters; and both sets of characters act together in securing the difference in delay of the two seeds.

Temperatures fluctuating between 25 and 40° are apparently no more effective in producing germination than the constant high temperatures employed. Since the pressure in the germinators remains constant while the vapor pressure fluctuates with the temperature, it is evident that the oxygen pressure fluctuates also, and that its fluctuation is inversely as the temperature, rising as the temperature falls, falling as the temperature rises. CROCKER found such fluctuating temperatures more effective in producing germination than constant temperature of 35° in the upper seeds with testas intact. The fluctuation may render the testa more permeable to oxygen, but in view of the effect of temperature on oxygen demand, the inference cannot be made with certainty.

A peculiar result was observed in all the control experiments at high temperatures. At normal room temperature, both the experimental seeds and the controls show less growth in the uppers than in the lowers; but at high temperatures, whether constant or fluctuating, this relation is reversed in the controls. This is noticed on comparison of lower and upper controls in table II. At the same time, both lowers and uppers of the experimental seeds show less growth in a fluctuating temperature of 25–40° than corresponding lowers and uppers at constant high temperature of 31° and equal pressures. The first two experiments in table II, com-

pared with the two fluctuating experiments in the same table, show this to be true. The decreased growth in the fluctuating temperature in this case is possibly due partially to the decreased oxygen pressure in the germinators as the vapor pressure increases with the rise in temperature.

PRESSURE AND THE OXYGEN MINIMUM

The method employed in these experiments has been briefly described, and the results are recorded in table III. Parallel experiments at reduced pressure were run along with the hydrogen tests, the germinators being kept in the same running water at a pressure of 85 mm. The oxygen pressure in the hydrogen and reduced pressure experiments would have been the same but for the aqueous pressure in the latter. The correction for water vapor reduces the O_2 pressure from 17.79 mm. to 14.39 mm., a large enough difference to make the results not directly comparable. The first three tests were with *X. pennsylvanicum*, the remainder with *X. glabratum*.

The first of these hydrogen tests is of little value in determining the effect of pressure on the oxygen minimum, for the oxygen content was 35.25 mm., or more than double that used in any of the reduced atmospheres. Only a slight reduction of the growth is brought about, which would indicate that this amount is probably somewhat below the optimum oxygen pressure for *Xanthium*. NABOKICH has shown that the atmosphere contains considerably more than the optimum oxygen supply for growth in higher plants.

On comparing the results of the remaining hydrogen tests with those at reduced pressures, it is seen at once that there is a higher percentage of germination, and a greater average growth in the hydrogen than in the reduced atmosphere. For instance, in hydrogen 96.6 per cent of the lowers, and 43.3 per cent of the uppers of *X. pennsylvanicum* germinated, as compared with 26.6 per cent of the lowers and 23.3 per cent of the uppers in the 85 mm. atmosphere. *X. glabratum* shows a similar behavior, 56.6 per cent of the lowers, and 23.3 per cent of the uppers germinating in the reduced atmosphere. Is this difference due to a difference in oxygen pressure

TABLE III

DURATION OF EXPERIMENTS 10 DAYS

MANOMETER PRESSURE (MM.)	PERCENT OF OXYGEN IN HYDROGEN	AQUEOUS PRESSURE (MM.)	ATMOSPHERIC PRESSURE (MM.)	OXYGEN PRESSURE (MM.)	TEMPERATURE (C.)	PERCENTAGE OF GERMINATION				AVERAGE GROWTH IN LENGTH OF HYPOCOTYL (MM.)			
						Lowers	Controls	Uppers	Controls	Lowers	Controls	Uppers	Controls
	4.70	.....	.....	35.25	21.5–22.5	93.3	86.6	93.3	83.3	94.3	101.8	89.25	105.0
	2.34	.....	.....	17.55	21.5	96.6	93.3	43.3	100	81.8	103.64	47.0	94.9
85.....	....	16.25	68.75	14.39	21.5	26.6	93.3	23.3	100	36.1	103.64	33.9	94.9
85.....	....	16.35	68.75	14.39	21.5	56.6	93.3	23.3	100	42.8	103.64	10.5	94.9
	2.34	.....	.....	17.55	22.0	93.3	100	30.0	100	77.8	88.2	43.2	82.4
85.....	....	16.25	68.75	14.39	22.0	53.3	100	13.3	100	34.0	88.2	19.0	82.4
85.....	.....	16.25	68.75	14.39	22.0	90.0	100	13.3	100	38.1	88.2	26.0	82.4

alone, or does the difference in pressure as such have a part in producing this effect? Comparison of the results in hydrogen gas with those at 90 and 99 mm. in table I, which approach most nearly the same oxygen pressure, shows that the difference is probably nearly all due to difference in oxygen pressure, rather than to a difference in barometric pressure. It is possible that great reduction in pressure may affect slightly the percentage of germination and the amount of growth. WIELER (**28**) came to the conclusion that growth is independent of pressure; and SCHAIBLE (**25**) observed that reduced pressures increase the rate of growth, but that the influence of air pressure on germination is very slight.

From the data of table III, as compared with the results of the other experiments, it appears that the oxygen minimum is practically the same for any given temperature, whether the reduction is accomplished by reducing the atmospheric pressure, or by dilution with inert gases like hydrogen.

AFTER-RIPENING OF XANTHIUM

Several attempts have been made to test the after-ripening of *Xanthium* seeds, with the results here briefly recorded. During October and November 1910, I made a test of the germination of *X. glabratum* at normal pressure, average temperature 23° C., at Transylvania University. Seeds in three different stages were taken as follows: green seeds, so young that the testas were still quite white; seeds which had ripened normally on the plants in 1910; seeds collected in the same locality in 1909. The seeds were prepared for germination as in all the other tests, and the integuments removed carefully. The results show that, at normal pressures at least, the protoplasm does not pass from an inactive state to an ultimately more active one, and that there is no after-ripening in that sense. The seeds averaged as follows in growth in length:

	Lowers	Uppers
1910 green seeds	46.0 mm.	37.0 mm.
1910 brown seeds	36.0 mm.	31.5 mm.
1909 brown seeds	34.3 mm.	30.35 mm.

One experiment with fresh seeds at reduced pressure agrees with these results. The seeds were kept at 90 mm. pressure. tempera-

ture 21.5°, December 2–11, 1909. In this case 96 per cent of the lowers, and 33 per cent of the uppers germinated; and the lowers averaged 30 mm. in length, the uppers 10 mm. The controls were injured in some way, but all had germinated. A comparison of these figures with those at 90 mm. pressure, temperature 21–22.6° (table I), using seeds almost a year old, shows that fresh seeds have as high a percentage of germination and a more rapid growth than the old seeds under reduced pressure.

In another experiment, however, seeds collected green in 1910 were tested along with seeds a year old, and no germination was secured at 90 or 100 mm. pressure, at 21°, in either crop of seeds. In the controls growth was fine, and the 1910 seeds showed a better growth than the 1909, just as reported above for seeds germinated under the same conditions.

It is possible that the after-ripening manifests itself in a change, either in the lowered demand of the embryo for oxygen, or in an increased permeability of the coats to oxygen, or in both at once, the change being too slight to affect the results at normal pressure. Some experience with these seeds in laboratory exercises in the Hull Botanical Laboratory lends force to this suggestion. With freshly ripened seeds having the testas intact, the classes fail to get the usual cotyledonary germination in pure oxygen atmosphere, as was reported by CROCKER for the upper seeds of *X. canadense* after 6 days at 21–23°; but in the winter, several months after ripening, these same seeds gave good cotyledonary germination in pure oxygen. This experience indicates either a decrease in the demand for oxygen by the seed, or an increase in the permeability of the seed coats as ripening progresses, and corroborates the evidence furnished by the experiments on after-ripening.

It is clear from these experiments that there is a slow progressive deterioration of the seeds, manifested in the reduced growth of the seeds as they become older, which after a few years probably causes entire loss of power to germinate. This deterioration seems to be a little more rapid in the lowers than in the uppers, but the physiological difference of the two seeds was very evident in the oldest seeds, and no doubt remains so long as they will germinate at all.

Discussion

The methods employed in much of the recent work on delayed germination of seeds has not been as exact as is desirable, or even necessary, for the solution of the problems involved in this phenomenon. The factors which are influential in the germination behavior have been investigated qualitatively only, without any attempt to measure them accurately and determine their relations. Moreover, the seed has been regarded too often as an embryo only, which may be affected profoundly by chemical and ethereal stimuli, the testa being considered as negligible on account of its thinness or on other insufficient grounds. In KINZEL's latest paper (**16**) he claims to have met all the serious criticisms made against his work, but in none of his experiments has he eliminated the testa as a factor. Recently LEHMANN (**17**) has shown that other stimuli than light can be substituted in its place and produce approximately the same effect. For instance, he found that the effect of 1 per cent Knop's solution in the germination of the seeds of *Ranunculus sceleratus* was much the same, inducing practically the same percentage of germination. If such substitutions of stimuli are possible, what can be stated with certainty as to the cause of delay in these cases? Light and the chemicals undoubtedly affect something, but it may as easily be the testa as the embryo that is changed. Even if the effect is actually produced in the embryo in these instances, the phenomena are not explained by saying that the protoplasm has been rendered "lichthart" or "lichtmüde," as if it were a sort of "weariness of the flesh!" If there is a change in the permeability of the embryo, or other physical or chemical alterations in it which leads to activity or cessation of activity, demonstration of such changes would throw some light on the phenomena.

In these *Xanthium* experiments the determinations have been made with as great exactness as possible, the accuracy lying well within the variability of the seeds themselves, and the work has been almost entirely quantitative. These methods demonstrated clearly the physiological difference between the embryos of the upper and lower seeds, although the difference is so slight as not to affect visibly the germination of the uppers at atmospheric pressure when the testa has been removed. This fact shows the value

of the quantitative method. It may reveal differences existing in various parts of the seed, which would otherwise remain undiscovered, and may in this way lead to results of the highest significance in the explanation of delay in germination. Often only quantitative measurements can detect the factors which determine the peculiarities of behavior.

The oxygen pressure needed to initiate germination in *Xanthium* seeds with coats removed is considerably less than would be expected in view of the rapid exchange of gases which CROCKER found in these seeds with testas intact. However, the amount necessary is large in comparison with the oxygen supply needed by seeds of many other angiosperms. The question as to whether higher plants can grow in absence of oxygen has been much discussed recently. Attention was called to the results of TAKAHASHI on rice, of CROCKER on *Alisma* and *Eichhornia*, of NABOKICH and LEHMANN on the organs of the seeds of many higher plants, in the introduction to this paper. NABOKICH believes that the organs of nearly all seeds of higher plants can grow in absence of free O_2. *Xanthium* seeds would certainly have afforded him a remarkable exception. It is much more probable, from the data now before us, that the seeds of the higher plants vary largely in the amount of oxygen required for germination, some of them, like *Alisma Plantago-aquatica*, rice, and other seeds which grow in media containing little free oxygen, requiring no free oxygen whatever; others, like *Xanthium*, requiring a comparatively large amount; with perhaps the great majority of seeds lying somewhere between them in regard to oxygen need. Such seeds as water plantain stand at the one end of the series, and *Xanthium* perhaps at the other extreme, with all possible intergradations. The experiments which have been carried on with *Xanthium* show that some seeds require a comparatively large amount of free oxygen, thus making each species of seed a problem in itself. There is no one behavior for the seeds of all higher plants, as NABOKICH seems to believe.

There are several facts which need to be considered in connection with the apparent inconsistency between the results I have obtained with *Xanthium* seeds as to the need for oxygen when the

testa has been removed, and those obtained by CROCKER with the same kind of seeds with the testa intact. When the seeds with testas on are allowed to germinate normally, the hypocotyl always elongates first and the root is well developed before the cotyledons begin to grow. That is, there is a strong correlation between the growth of these two organs of the seed. But if the well ripened seeds with coats on are germinated in an atmosphere containing a high percentage of oxygen, the cotyledons instead of the hypocotyl initiate the development of the embryo. The strong normal correlation is reversed by temporary suppression of the hypocotyl, due probably to a more rapid diffusion of oxygen through the very thin distal portion of the testa surrounding the cotyledons than through the thick proximal portion which invests the hypocotyl. The cotyledons thus receive the necessary free oxygen for germination sooner than the more sensitive hypocotyl, with the result that the usual course of growth in the seed is completely changed.

This reversal of a very strong correlation probably requires considerably more oxygen than a normal germination. Not only is the usual behavior overcome, but the part which grows instead of the hypocotyl is a much less sensitive part of the embryo, undoubtedly requiring more oxygen to initiate its activity. In animal cells food storage renders the protoplasm inert, and delays cell division to a very marked degree. It is possible that food storage in the cotyledons has a similar effect on their activity, requiring more energy, and therefore more oxygen, for the growth processes.

Another factor probably responsible for a considerable portion of the gaseous exchange during germination with the seed coats intact is the testa itself. BECQUEREL (**2**) has shown that the integuments of seeds produce CO_2 in comparatively large amounts, sometimes greatly exceeding the seeds from which they have been taken in CO_2 production. For instance, he found that one gram of *Ricinus* integuments exposed to light gave off 18 times more CO_2 than one gram of seeds with testas removed; that one gram of the testas of *Vicia Faba* gave off 10 times as much CO_2 as the same weight of decorticated seeds; and that one gram of the coats of the pea produced 25 times as much CO_2 as a gram of the embryos.

In CROCKER'S experiments the measurement of the gaseous exchange was made for seeds with testas on, and therefore included whatever coat CO_2 production occurred. And, since the thickness of the testa over the hypocotyl practically excludes the oxygen from that organ, while the thinner distal portion of the coat admits the oxygen to the cotyledons first, thus initiating the cotyledonary germination mentioned above, the measurement of the gaseous exchange has dealt very largely with that occurring in the cotyledons. In my experiments the removal of the coats eliminates the coat CO_2 production; and, since the cotyledons never grow under the conditions of the experiment until after the hypocotyl has elongated, the determination of the oxygen minimum is made for the hypocotyl only. There is no inconsistency, I believe, between the results obtained by CROCKER and those obtained in these experiments. Indeed, the unusually high minimum for the decorticated seeds agrees well with the data secured in earlier determinations with the coat intact, when the coat CO_2 production and the reversal of the correlation between hypocotyl and cotyledons are taken into consideration.

The lowering of the oxygen minimum by increase of temperature is at least partially accounted for by the increase in anaerobic respiration as the temperature rises. On the other hand, if a constant free oxygen supply below the optimum is maintained during a rise in temperature, the growth capacity of the organism is increased as the temperature rises. It is known, also, that merely cutting off the supply of oxygen will increase the anaerobic respiration in many organisms. With the oxygen reduced to a minimum, and at the high temperature employed, the conditions in these experiments are favorable to a considerable increase in the anaerobic form of respiration. As the anaerobic respiration increases, there is less need of the aerobic to release the energy sufficient to initiate growth. The question then naturally arises whether the lowering of the oxygen minimum by increasing the temperature really indicates any difference in the amount of respiration occurring. It is possible that the total energy release necessary for the germination of the seed is practically the same at any given temperature, the variation being in the proportion of release due to aerobic

and anaerobic respiration. This question can be answered only by further investigation.

A detailed study of the permeability of the seed coats of *Xanthium* to oxygen and other gases and reagents will be carried on, with the purpose of determining whether BECQUEREL'S conclusions regarding the rôle of dry seed coats have general applicability.

The necessity for more exact quantitative studies of the factors which cause delayed germination is emphasized by this work. The factors which cause specific behavior of the seed are sometimes very minute and may escape detection entirely unless the methods employed in investigation are adapted to that end. The most refined methods of quantitative study are best suited to this purpose, and for a further advance with the problems of delayed germination it will be necessary to adopt the most exact and rigorous methods of analysis.

Summary

1. The naked embryos of the dimorphic seeds of *Xanthium* exhibit a marked difference in their demand for oxygen for germination.

2. The oxygen minimum for the germination of decorticated *Xanthium* seeds at 21° C. is approximately 12 mm. for the upper seeds, and about 9.5 mm. for the lowers.

3. Increasing the temperature decreases the minima, a rise of 10° from 21° lowering the necessary minimum of oxygen from 12 mm. to approximately 7 mm. for the uppers, and from 9.5 mm. to approximately 3 mm. for the lowers.

4. Variation of the total atmospheric pressure probably does not influence the oxygen minimum for germination. The experiments indicate that equal partial pressures of oxygen produce approximately the same effect on the seeds, regardless of the total pressure of which it forms a part.

5. There is very little after-ripening, or at least the after-ripening is not visible in an altered germination behavior at atmospheric pressure and ordinary temperatures. There is evidence either of a decrease in the oxygen need, or an increase in the permeability of the coats to oxygen, or both, as ripening progresses.

6. A very slow progressive deterioration of the seeds takes place, which after a few years causes entire loss of power to germinate.

7. The general conclusion that the organs of the seeds of higher plants can grow in entire absence of free oxygen is not supported by the results obtained with *Xanthium* seeds. They cannot grow without comparatively large amounts of free oxygen.

8. The oxygen pressures required for germination of *Xanthium* seeds are very much higher than those reported by LEHMANN for the epicotyls of such plants as *Helianthus perennis*, *Zinnia elegans*, and *Glyceria fluitans*.

9. Since the coats cause delay by excluding oxygen, we might expect to find the oxygen demand for growth high. *Xanthium* seeds stand at the opposite end of the series from the seeds of certain aquatic plants, as water plantain and rice, in demands for oxygen for germination.

10. The high oxygen demand, and the difference in this demand in the two seeds, act with the coats to secure delay, and a difference in delay, in the two seeds. But if the coat has been removed, the demand for oxygen by the embryo is too low to be significant in securing delay in germination.

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BRIEFER ARTICLES

A PROTOCORM OF OPHIOGLOSSUM

(WITH ONE FIGURE)

In October 1908, Dr. CHARLES R. BARNES and the writer, while collecting bryophytes in a little known region of Mexico, botanically speaking, on the eastern edge of the great central plateau, about 150 miles northeast of Mexico City, on the boundary of the states of Hidalgo and Puebla, found great quantities of an *Ophioglossum*, which was distributed as *O. Pringlei* Underwood by the late Dr. C. G. PRINGLE.[1] The plants were in such numbers and varied so much in size that some days were spent in a thorough exploration of the region, hoping to find gametophytes. Of many hundred small plants, only one showed anything resembling a prothallus. After returning to Chicago, this supposed prothallus was sectioned and found to be a protocorm.

The protocorm, buried in the soil to a depth of 5 cm., is almost spherical and 9 mm. in diameter (fig. 1), with a slightly roughened surface caused by the irregular collapse of dead cells of the outer cortex. The leaf, including the petiole, is 13.5 cm. long, and shows no trace of a fertile spike. The remains of the leaf traces of five other leaves are present, showing that the protocorm is at least seven years old. The growing point is sunken in a pit made by cortical upgrowth. Numerous rootlets are penetrating the cortex in all directions, but only three or four in the upper region of the corm have reached the soil, and have partly decayed. The outermost cells of the cortex have lost their contents and collapsed, forming a protecting layer. These empty outer cells, as well as those of the partly decayed rootlets, are infested with fungal hyphae, which, however, do not enter the living cortical cells. The cells of the cortex are very full of starch.

[1] The specimens were submitted to Dr. J. M. GREENMAN, who has made the following statement in reference to them: "Upon comparison of the material in collections determined as *O. Pringlei* with known species of this genus, I am unable to find a single character to separate it from our northern species *O. vulgatum* L. So far as I can find, *O. vulgatum* never has been definitely recorded from Mexico, but we have it represented from different stations from Canada and Maine to Arizona, and it would not be unparalleled by other cases to have it turn up in Southern Mexico. I should be inclined, therefore, to regard these Mexican specimens as conspecific with *O. vulgatum* L."

It was noticed that the plants with few exceptions were in groups of 3–10, usually radiating from a large plant. When the root system of these groups was laid bare, a work of no little difficulty because of the depth of the roots and the great number of roots of other plants in the soil, it was found that nearly all of the plants of a group were connected, and that the smaller plants were produced by adventitious budding of the roots of the larger plants. This method of vegetative reproduction is found in several species of *Ophioglossum*. Occasionally a leaf bears two fertile spikes.

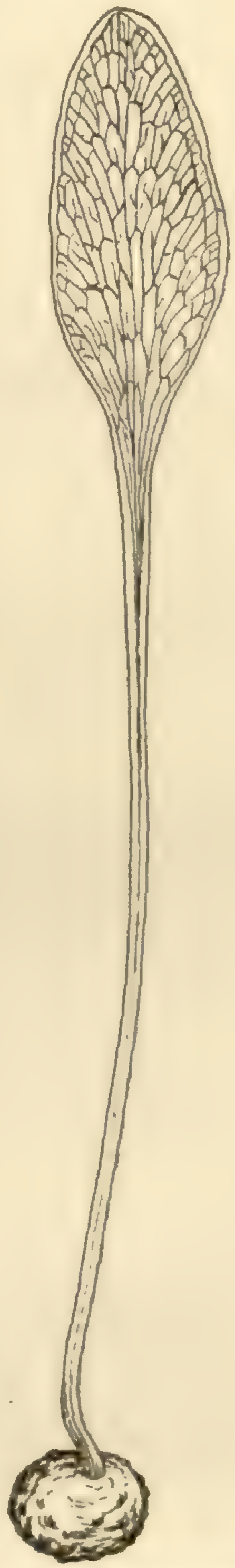

FIG. 1.—*Ophioglossum:* protocorm bearing sterile leaf.

The presence of a protocorm, and a method of vegetative reproduction so similar to *Phylloglossum*, may lead the unwary, or the "arm chair" botanist, to speculate concerning a possible relationship between Ophioglossales and Lycopodiales. It must be borne in mind that the protocorm probably has no phylogenetic significance whatever.

The region is one of exceptional interest to a botanist. The great central plateau falls sharply away to the low plain bordering the Gulf of Mexico. Rain and mist are abundant even in the dry season, because the clouds drift against the high eastern escarpment of the plateau. The border of the plateau is deeply dissected by the numerous small streams which fall over its edge and form box cañons, sometimes 500 meters deep. Because clouds continually drift up these cañons, their walls and floors are covered with dense masses of filmy ferns, liverworts, and mosses. On the high mesas between these cañons, but never in them, this *Ophioglossum* is most abundant. In the same situation *Lycopodium clavatum* and *L. complanatum* are also abundant. The species of *Lycopodium* and *Ophioglossum* are apparently confined to an altitude of about 2200 meters. At the same altitude, on the bank of a stream just before it plunges over the wall of a box cañon, a bog of volcanic ash and sphagnum was found.—W. J. G. LAND, *The University of Chicago*.

CURRENT LITERATURE

MINOR NOTICES

Trees and shrubs.—Part III of the second volume of this work has been issued,[1] and contains full and lucid descriptions of some 30 species, 25 of which are accompanied by carefully executed full-page illustrations, including detailed drawings of flowers and fruit. Nearly all of the plants considered are native in the South Atlantic and Gulf states, and about one-half of the species treated are new to science. New species are published in the following genera: *Quercus* (1), *Hamamelis* (1), *Crataegus* (3), *Prunus* (6), and *Sambucus* (1). The high standard of excellence, characteristic of the previous parts, is fully maintained in the present issue.—J. M. GREENMAN.

Flora of Congo.—A second fascicle[2] of the third volume of this work has appeared recently, which records the results of further studies in several families of spermatophytes from the Gramineae to the Compositae. A number of species new to science are included, described, and illustrated in the same excellent manner as in previous fascicles of this flora.—J. M. GREENMAN.

NOTES FOR STUDENTS

Experiments with maize.—Several years ago BLARINGHEM[3] published a monograph on his now well known experiments in the production of anomalies in various plants as the result of mutilation. The mutilations forced into development buds which ordinarily remain latent, and the branches produced from these buds frequently possessed characters not recognized as normal features of the plants operated on. In a small percentage of cases the abnormalities thus brought to light were found to be inherited to a greater or less degree, and the conclusion was reached that mutilation is a very general and easy means of provoking mutability and an important factor in the evolution of vegetable forms. Most of his experiments were made with maize, though some apparently corroboratory evidence was derived from barley (*H. distichum* and *H. tetrastichum*) and mustard (*Sinapis alba*). All of the new characters, abnormal or otherwise, which came to light in his experiments with maize

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[1] SARGENT, CHARLES SPRAGUE, Trees and shrubs. Illustrations of new or little known ligneous plants, etc. 4to, pp. 117–190. *pls. 151–175*. Boston and New York: Houghton Mifflin Co. 1911. $5.00.

[2] DE WILDEMAN, ÉMILE, Flore du Bas- et du Moyen Congo. Ann. Mus. Congo Belge. Bot. V. **3**:149–316. *pls. 28–49*. 1910. Brussels.

[3] BLARINGHEM, L., Mutation et traumatismes. Étude sur l'évolution des formes végétales. pp. 248. *pls. 8*. Paris: Felix Alcan. 1908.

were discovered in the descendants of one original plant mutilated by the author in 1902. After that time the pedigrees were kept carefully controlled, either by hand-pollinations or by cultivation in isolated plots.

The reviewer,[4] at about the time this monograph appeared, demonstrated the occurrence of numerous biotypes in hybrid combination in what appeared to be a fairly uniform population of maize, and believes this to be the general situation in this species. JOHANNSEN[5] has pointed out that the reviewer's results favor a different interpretation of BLARINGHEM's experiences, since the new types which proved to be hereditary may have appeared as the result of segregation of biotypes which were already present in the original plant chosen for mutilation, this segregation being due, not to the mutilation, but to the subsequent method of breeding. GRIFFON[6] has given further support to this interpretation of BLARINGHEM's results, by showing that similar abnormalities appear when no mutilations have been practiced, and the reviewer has had the same experience. GRIFFON shows that the abnormalities which characterized BLARINGHEM's forms are strongly dependent upon seasonal conditions for their development, being much more abundant in all cultures in some seasons and less abundant in all in other seasons. He does not agree with BLARINGHEM that with respect to these abnormalities these maize families constitute ever-sporting varieties. It does not follow, however, that abnormalities are not hereditary because they are strongly affected by the environment. HUS and MURDOCK[7] have shown the inheritance of fasciation in a strain of popcorn, the offspring of two fasciated ears giving progenies over 50 per cent of which produced fasciated ears, while an unfasciated ear from the same strain gave only 3 per cent fasciated ears. It will be understood, of course, that the strain from which these ears were selected was complexly hybrid, and that pure-bred derivatives might have shown either approximately 100 per cent fasciated or approximately no fasciation, under favorable conditions. There is evidence that the fasciation is strongly fluctuating, the two ears on a single stem being not infrequently one fasciated and the other normal. The significance of the percentage inheritance is doubtful in complex material of this kind.

The reviewer[8] has presented additional evidence of the hybrid nature of ordinary vigorous maize plants, and their dependence for their vigor upon

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[4] SHULL, G. H., The composition of a field of maize. Report Am. Breeders' Association **4**:296–301. 1908.

[5] JOHANNSEN, W., Elemente der exacten Erblichkeitslehre. pp. vi+516. *figs. 31.* Jena: Gustav Fischer. 1909. See p. 451.

[6] GRIFFON, E., Observations et recherches expérimentales sur la variation chez le maïs. Bull. Soc. Bot. France **57**:604–615. 1910.

[7] HUS, H., and MURDOCK, A. W., Inheritance of fasciation in *Zea Mays*. Plant World **14**:88–96. 1911.

[8] SHULL, G. H., Hybridization methods in corn breeding. Amer. Breeders' Mag. **1**:98–107. 1910.

this hybridity. Previous conclusions that F_1 hybrids between self-fertilized strains are on the average equal in yielding capacity, and in certain combinations much superior, to strains cross-bred in the normal manner, have been confirmed; also that reciprocal crosses are essentially equal. In addition it is shown that the yield and quality of the crop are functions of the particular hybrid combination, the results being the same whenever the cross is repeated. The F_1 was found no more variable than the pure self-fertilized parental strains, but the F_2 was considerably more variable, the coefficients of variability in number of rows on the ears in pure biotypes and in their F_1 hybrids being respectively 9.081 per cent and 9.063 per cent, while that of the F_2 was 12.63 per cent. This greater variability in the F_2, also noted by EMERSON[9] in respect to size of seeds and height of stalks, though the latter gives no coefficients, clearly demonstrates the segregation of different grades of such purely quantitative characters. EAST[10] has also presented similar evidence of the segregation of a quantitative character (height of stalk) in the F_2, but he makes no reference to the reviewer's corresponding results published a year earlier. He gives no coefficient of variability for pure strains, but his coefficient for the F_1 was 8.68 per cent, while in the several F_2 families it ranged from 12.02 per cent to 15.75 per cent.

The theory that the increased vigor of cross-bred maize plants is due to a stimulation accompanying heterozygosis requires that crossing within the same biotype or within the same F_1 shall give no advantage over self-fertilization in the same biotype or in the same F_1. The reviewer[11] has reported on a number of such sib-crosses in comparison with corresponding self-fertilizations, the advantage in favor of the crosses being so slight that they can be fairly accounted for by the lack of complete genotypic purity in some of the self-fertilized families. Crosses between sibs in ten self-fertilized families had an average height of 20 dm. and gave an average yield per acre of 30.17 bushels as compared with a height of 19.28 dm. and a yield of 29.04 bushels in the offspring of self-fertilized parents. In the F_2 those families which sprang from sib-crosses in the F_1 had an average height of 23.30 dm. as compared with 23.55 dm. in families produced from self-fertilized parents, and the corresponding yields per acre were 47.46 and 41.77 bushels respectively. These results show that cross-fertilization is of no (or little) advantage except when it brings together unlike hereditary elements. The relations of F_1 and F_2 in regard to height of plants and yield per acre strikingly emphasize the economic importance of using hybridized seed corn. Ten F_1 families had an average height of 25 dm. and produced an average yield of 68.07 bushels,

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[9] EMERSON, R. A., The inheritance of sizes and shapes in plants. Amer. Nat. **44**:739–746. 1910.

[10] EAST, E. M., The genotype hypothesis and hybridization. Amer. Nat. **45**: 160–174. *figs. 6.* 1911.

[11] SHULL, G. H., The genotypes of maize. Amer. Nat. **45**:234–252. *fig. 1.* 1911.

while twenty corresponding F_2 families had an average height of 23.42 dm. and gave a yield of only 44.62 bushels per acre.

HAYES and EAST[12] have also shown a similar relation between first and second generation crosses, one such cross giving 105.5 bushels per acre in F_1 and only 51.5 bushels in F_2, another cross giving respectively 117.5 bushels per acre and 98.4 bushels per acre. These authors give a good discussion of the economic bearings of these results and methods of putting them to practical use.

COLLINS[13] has also shown the practical value of hybridization methods in corn growing, reporting on the results of sixteen rather wide crosses, all but two of which gave higher yields than the average of the parents, and all but four exceeding the better parent in yielding capacity. PEARL and SURFACE,[14] while subscribing to the correctness of the genotype idea as applied to maize, are of the opinion that the ordinary ear-to-the-row selection method "in a much cruder and less precise way, really makes use of the same principle" as the reviewer's "pure-line method," and they advocate simply the relaxation of the selection after a few years, by which time the "more strikingly undesirable genotypes will have been automatically eliminated." This view fails to take account of the relatively greater vigor in the F_1 hybrids. EAST,[15] HAYES and EAST,[16] and COLLINS,[17] on the other hand, urge the use of the method of MORROW and GARDNER,[18] as the most practical means of utilizing the greater vigor produced by heterozygosis, and the reviewer believes that the attitude of these authors is justifiable. The method of MORROW and GARDNER is identical with the "pure-line" method, except that highly developed commercial varieties are used in the place of pure self-fertilized strains. The two chosen parental types are grown in alternate rows in an isolated plot, and one variety is detasseled. The seed for the general crop is harvested from the detasseled row, and the process is repeated year after year, using the same parental varieties.

EAST and HAYES[19] have made a most important contribution to knowledge

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[12] HAYES, H. K., and EAST, E. M., Improvement in corn. Bull. Conn. Agr. Exp. Sta. pp. 21. *pls.* 4. 1911.

[13] COLLINS, G. N., The value of first-generation hybrids in corn. Bull. 191, B.P.I., U.S. Dept. Agr. pp. 45. 1910.

[14] PEARL, R., and SURFACE, F. M., Experiments in breeding sweet corn. Ann. Rep. Maine Agr. Exp. Sta. 1910.. pp. 249–307. Bull. 183. *figs.* 220–233.

[15] EAST, E. M., The distinction between development and heredity in inbreeding. Amer. Nat. **43**:173–181. 1909.

[16] *Op. cit.* [17] *Op. cit.*

[18] MORROW, G. E., and GARDNER, F. D., Field experiments with corn 1892. Bull. 25, Ill. Agr. Exp. Sta. pp. 173–203. 1893.

[19] EAST, E. M., and HAYES, H. K., Inheritance in maize. Bull. Conn. Agr. Exp. Sta. pp. 137. *pls.* 25. 1911.

of the inheritance of unit characters in maize, and have succeeded in clearing up most of the difficulties met by CORRENS and LOCK, and simply by the expedient of applying a strictly *individual* analysis, instead of permitting pollinations from a number of individuals possessing the same characteristics. Only a few of the more striking results can be mentioned. There are two independent genes for yellow endosperm color, giving F_2 ratios 3:1 and 15:1. These are so related as respects dominance that the intensity of the yellow color agrees approximately with the actual number of Y genes present, i.e., the color is most intense in seeds having both genes homozygous, less intense when one gene is homozygous and the other heterozygous, still less intense when both are heterozygous or when either is absent and the other homozygous, etc. This situation results in a distribution of individuals in the form of the probable error curve, and is therefore superficially like that of fluctuating variations, from which it differs however in that the different grades are inherited. In another paper the senior author[20] makes use of these facts in extending Mendelian theory to include variation that is apparently continuous. In the purple aleurone color, EAST and HAYES find no less than four independent genes involved in different varieties, a full purple color requiring the simultaneous presence of both P and C, a full red color the presence of R and C. In the absence of C, both P and R are capable of producing some pigment, giving "particolored" seeds. In addition to these three genes, there was found in a cross between Tom Thumb pop corn and Black Mexican sweet corn, a factor which partially or wholly inhibited the production of the purple aleurone color. This inhibitor or "dominant white" is strictly normal in its hereditary behavior, and its presence in some of LOCK's strains undoubtedly accounts for that investigator's aberrant results. In pericarp colors the authors recognize five independent red-producing genes, R_1 the ordinary red of "red" maize, R_2 the striped red of "calico corn," R_3 a dirty red most abundant at the base of the grains and apparently completely coupled with red silks, R_4 and R_5 a rose red which reaches full development only on exposure to the sunlight. The red cob-color is a simple Mendelian dominant, independent of pericarp color. While starchiness is an endosperm character and shows xenia, the quality of the starch, whether flinty or floury, is a "plant character," and affects all the grains of an ear. Crosses between flint and dent varieties show undoubted segregation with the flint character recessive, but there are probably several genes involved, and the results are obscured by physiological correlation. Further evidence is given that size characters, such as height of stalk, length of ear, and size of grains, segregate normally in the F_2. Several abnormalities are mentioned, dwarfness, striped leaves, split and furrowed cobs, branched ears, and hermaphrodite flowers. With exception of the last, these characters are thought to be inherited in Mendelian fashion, though the

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[20] EAST, E. M., A Mendelian interpretation of variation that is apparently continuous. Amer. Nat. **44**:65–82. 1910.

possibility is suggested that fasciation of the ears may be a purely physiological effect of disturbed nutrition.

EMERSON[21] reports the discovery of red aleurone color as a latent character in a cross between Queen's Golden pop corn and Black Mexican sweet corn, though other crosses between these two varieties gave only purple aleurone. Crosses between a tested homozygous red-aleurone strain and White Rice pop corn and Evergreen sweet corn produced F_1's with only purple aleurone cells, thus demonstrating the presence of *P* as a latent character in both of these white varieties. Dark and light yellow endosperm colors were also seen to be latent as a result of a cross between the orange-colored Queen's Golden and the Black Mexican with colorless endosperm.

While not experimental, two papers by ILTIS[22] on abnormalities are worthy of mention. Both of these abnormalities are assumed to have been induced by the traumatic action of *Ustilago Maydis*. In the first the glumes of the female flowers were somewhat enlarged, and in place of the carpel arose a tubular structure 10–20 cm. long, terminated by a long pistil-like thread 20 cm. long. The occurrence of a ligule on this structure served to identify it as a phyllode, and leads the author to the conclusion that the ovary, which afterward forms the seed coat, is homologous with the leaf sheath, and the style with the leaf blade. Within this tube, as a prolongation of the axis, grew an abnormal leafy branch. In the second paper[23] the author describes abnormal inflorescences in which the flowers are paired, each pair consisting of a sessile female or hermaphrodite flower and a stalked male flower. This is an arrangement characteristic of the Andropogoneae, and the author looks upon its appearance in maize as a reversion. On this basis he would rank the Zeae as a subtribe of the Andropogoneae, in support of HACKEL and STAPF, who had adopted this arrangement on other grounds.—GEO. H. SHULL.

Lichen parasites.— TOBLER[24] has studied the relation of two so-called lichen parasites to the lichen host, to the alga on which the lichen grows, and to the substratum to which the lichen is attached. After the manner of thinking commonly followed by European botanists, and often by American as well,

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[21] EMERSON, R. A., Latent colors in corn. Ann. Rept. Amer. Breeders' Ass. **6**: 233–237. 1910.

[22] ILTIS, H., Ueber eine durch Maisbrand verursachte intracarpellare Prolifikation bei *Zea Mays* L. Sitzungsber. Akad. Wiss. Wien. Math.-naturw. Klasse **119**[1]. pp. 15. *pls. 2*. 1910.

[23] ILTIS, H., Ueber einige bei *Zea Mays* L. beobachtete Atavismen, ihre Verursachung durch den Maisbrand, *Ustilago Maydis* (DC.) Corda über die Stellung der Gattung *Zea* im System. Zeitschr. Abst. Vererb. **5**:38–57. *pls. 2*. 1911.

[24] TOBLER, F., Zur Biologie von Flechten und Flechtenpilzen. I. Ueber die Beziehungen einiger Flechtenparasiten zum Substrat. Jahrb. Wiss. Bot. **49**:389–409. *pl. 3. fig. 1*. 1911.

he considers the lichen to consist of the fungus and the alga on which it grows, instead of accepting the logical view, namely, that the fungus alone constitutes the lichen.

Phacopsis vulpina Tul. and *Karschia destructans* Tobler, of the Pezizineae, are considered with respect to their biological relation to the lichens on which they grow and to the algal hosts of these lichens. *Phacopsis vulpina* is found on the thallus of *Evernia vulpina* (L.) Ach. in the Alps. By sectioning the fungus and the lichen host together in paraffin and subsequent treatment with iodine solution, the author was able to trace the course of the *Phacopsis* hyphae in the lichen thallus, and to prove that they reach the inclosed algal host cells, which they closely and often completely entwine. In places where the *Phacopsis* is best developed in the lichen thallus, the algae are entirely absent. In other portions of the lichen thallus the algae are surrounded singly or in groups by the *Phacopsis* hyphae, the *Evernia* hyphae being absent from such places. In other places the hyphae of both *Phacopsis* and *Evernia* are found entwining the algae. Thus it appears that the *Phacopsis* hyphae in time reach the algae in limited areas of the lichen thallus and gradually displace the hyphae of the latter. It seems that the algae multiply more rapidly for a time after the *Phacopsis* hyphae reach them, but may finally disappear entirely where these hyphae are most abundantly developed. When the *Phacopsis* hyphae have reached the region of the lichen thallus where the algae are found, they spread laterally until large portions of the *Evernia* cortex are cut off from the medulla within and finally die. The *Phacopsis* hyphae are found to penetrate into the dead cortex and into the medulla of the *Evernia*. The foreign hyphae are absent from the spermagonia of the *Evernia* and areas immediately surrounding them, but are present in the soredia, which may serve as portals of entry. The conclusion is reached that the *Phacopsis* is probably first a parasymbiont and later a parasite on the lichen thallus.

Karschia destructans Tobler is described from the thallus of the lichen *Chaenotheca chrysosephala* (Turn.) Th. Fr. It was found that the *Karschia* penetrates into and through the crustose thallus of the *Chaenotheca* and into the bark upon which the lichen thalli examined grew. In growing through the lichen thallus, the *Karschia* is found to entwine and destroy algal cells and to displace and destroy the lichen hyphae. This makes the *Karschia* a parasymbiont with the lichen and likewise a parasite on it. But finally, the *Karschia* hyphae penetrate into the bark, after which the fungus fructifies. So before the fungus produces its fruit, it becomes a saprophyte. Thus a parasitic, a parasymbiotic, and a saprophytic condition are found in one ontogeny. The author reaches the conclusion that the *Karschia* is for a time a lichen-fungus (we would say a lichen), but at other times a parasite or a saprophyte. Whether this fungus is a lichen is really a matter of definition; but whether a given plant should be called a lichen or not is of no special biological importance. If its relationship with the alga is accompanied by no morphological characters which should separate it from the genus *Karschia*,

the fungus must remain in that genus. Several other species of *Karschia* are numbered among about 400 fungi that grow on lichen thalli, and a study of each of these would be of special interest and value.

The author states that his study of these two fungi proves that there can be no sharp separation of the many fungi known to grow on lichens into parasites, parasymbionts, and saprophytes, since a single species may show all three conditions at various times in its life history. He thinks that further studies would demonstrate that most of the fungi found growing on lichens are not purely parasitic, but parasymbiotic and often saprophytic as well. In this he is probably correct, and further research along this line would add much to our knowledge of the biological relations of these fungi. The conclusion is also reached that these studies tend to obliterate the line of demarkation between lichens and other fungi. This is true, but a considerable number of botanists have already concluded that the biological distinction between lichens and other fungi should not serve longer to maintain the lichens as a distinct group in any general classification of plants.

Some other fungi growing on lichens were examined briefly, without adding materially to the important results secured in the study of the two species considered above.—BRUCE FINK.

Evolution of vascular structures.—In a bulky memoir of 325 pages, CHAUVEAUD[25] expounds his view of the evolution of vascular bundles as they are found in different groups of plants. He finds himself in disagreement with the current notion of the stele as a morphological concept of first importance, and returns to the earlier view of a vascular bundle as the unit. With him, in fact, a vascular bundle is either a xylem or a phloem group, and these are arranged according to one of six "*dispositions*": (1) centric, corresponding to protostele; (2) excentric, with the xylem group more or less flattened; (3) alternate, represented by a root with diarch structure; (4) intermediate, as seen in the hypocotyl of some plants; (5) superposed, a circular row of collateral bundles; and (6) peripheral, represented by amphivasal bundles such as are seen in monocotyledonous stems. Thus what most writers call a protostele is by CHAUVEAUD, as well as earlier writers, regarded as the most primitive condition; the alternate arrangement of xylem and phloem exhibited by all roots is the next main step in evolution; and from this root structure are to be derived the conditions seen in the stems of gymnosperms and angiosperms. It will be seen that this mode of derivation lays a heavy responsibility on the hypocotyl, for this transitional region is considered to reveal the stages in evolution leading to the stem structure of all the higher plants. One must swear entire allegiance to the recapitulation theory when adopting this scheme, although certain difficulties appear, for instance, in connection

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[25] CHAUVEAUD, G., L'appareil conducteur des plantes vasculaires et les phases principales de son évolution. Ann. Sci. Nat. Bot. IX. **13**: 113–438. *figs. 218*. 1911.

with the origin of amphivasal bundles. To some it may appear an unnecessarily round-about plan to derive a circle of collateral bundles from a protostele *via* the root, when direct routes have been proposed which do not violate the doctrine of recapitulation. Moreover, it would be interesting to see how the stele of *Osmunda* could be derived according to the new method, inasmuch as in ferns the evolution is said (p. 271) not to proceed further than the third or alternate disposition.

The memoir is divided into three parts, in the first of which a fairly complete historical résumé is given. This is rendered more valuable by the grouping of the papers under six headings. It is to be regretted that a number of errors have crept into the citations. The second part is devoted to a summary of the author's earlier researches in this field; while the third part contains an account of his new observations, extending over a wide range of vascular plants, including a large number of dicotyledons, though the critically important cases found in his group "vascular cryptogams" are represented only by *Pteris cretica*.—M. A. CHRYSLER.

Fermentation.—Experiments of HARDEN and NORRIS[26] confirm the work of other investigators according to whom many yeasts which ordinarily do not ferment galactose acquire the property of fermenting that sugar by being cultivated for a time on a medium containing it. The authors further show that the juice from such a yeast is also capable of fermenting galactose, and that the addition of phosphates to the fermentation-mixture causes an acceleration of fermentation similar to that observed in mixtures of glucose, fructose, or mannose and yeast juice on the addition of phosphates. As in the case of these hexoses, the phosphate is in the form of an organic compound from which it is not precipitated by magnesium citrate mixture. Small quantities of sodium arsenite also accelerated fermentation.

Regarding the constitution of the compound formed when a phosphate is added to a fermenting mixture of yeast juice and a hexose, three views have been proposed. According to HARDEN and YOUNG it is a hexose-phosphate containing two phosphoric acid residues. LEBEDEW holds that the compound contains only one phosphoric acid residue, basing his view on the fact that the ozazone obtained from it has only a single phosphoric acid residue. The third view is that of IWANOFF, who considers the compound a triose phosphate. In a recent paper, purely chemical in its content, but of great biological interest in so far as it clears up part of the mechanism of fermentation of sugars by yeast juice, YOUNG[27] presents further evidence to show that the compound is

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[26] HARDEN, A., and NORRIS, R. V., The fermentation of galactose by yeast and yeast juice (Preliminary communication). Proc. Roy. Soc. London B **82**:645–649. 1910.

[27] YOUNG, W. J., Ueber die Zusammensetzung der durch Hefepresssaft gebildeten Hexosephosphorsäure. II. Biochem. Zeitschr. **32**:177–188. 1911.

a hexose phosphate containing two phosphoric acid residues. The evidence is based largely on the composition of the barium salt of the compound, and on the behavior of its ozazones. In the formation of the ozazone, a single phosphoric acid molecule is split off, while the ozazone also contains a phosphoric acid residue.

It has been known that yeasts are able to ferment a number of substances other than sugars. The number of such substances which undergo a kind of fermentation accompanied by the evolution of carbon dioxide has been greatly extended by NEUBERG and TIR.[28] The substances which are fermented in this way by yeasts and yeast preparations are the common plant acids which occur naturally in fruit juices and other substances used in alcohol production, and also components or products of the yeast cell, as fatty acids, glycerine, and lecithin.—H. HASSELBRING.

Soil productiveness indicated by natural vegetation.—The practical object of SHANTZ'S Bulletin[29] on "Natural vegetation as an indicator of the capabilities of land for crop production in the Great Plains area" does not detract from its scientific value. It is an interesting and valuable example of the application of exact ecological research methods, with results establishing reliable data relating to the natural vegetation of a given region, and its correlation with the crop-producing capabilities of the land. Detailed investigations were made in Washington and Yuma Counties, Eastern Colorado, although a general survey included all the states of the Great Plains, a region containing the largest body of land of possible agricultural importance in the United States on which the native plant cover still exists. The methods included study of the vegetation with respect to the formations, dominant associations, and important species, and of the various determining factors with especial consideration of the physical conditions (temperature, rainfall, evaporation, saturation deficit, soil moisture, soil temperature, etc.). Records for these physical factors were made at 11 different stations on the Great Plains, under direction of BRIGGS, and supplemented by SHANTZ with many comparative observations. For purposes of comparison, the soil moisture determinations were reduced to definite standards, as moisture equivalent and non-available moisture (for Kubanka wheat).

Plant migrations, invasions, effects of fire, grazing, mowing, and other biotic agencies are considered. Illustrations of the root systems of significant species are given and their relations to the soils and in the successions are noted. Indicative of agricultural land are the grama-buffalo grass and the wire grass

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[28] NEUBERG, C., and TIR, L., Ueber zuckerfreie Hefegärungen. II. Biochem. Zeitschr. **32**:323–331. 1911.

[29] SHANTZ, H. L., Natural vegetation as an indicator of the capabilities of land for crop production in the Great Plains area. Bur. Pl. Ind. Bull. no. 201. pp. 100. *pls. 6. figs. 23.* 1911.

associations (both short grasses), also bunch grass and sand hills mixed (prairie grasses). Each of these types is characterized as to general appearance, floristic composition, correlated physical factors, effects of disturbing factors, variations from the typical association. The relationships and successions of the different associations are outlined, primary and secondary successions being recognized, though these do not appear to be fundamentally distinct. The remainder of the bulletin is concerned with crop production in the light of the data obtained, with practical suggestions as to the choice of land and to methods of culture.—LAURA GANO.

Embryo sac of Pandanus.—In 1908, CAMPBELL published a preliminary note on the embryo sac of *Pandanus*, and in 1909 a fuller paper appeared.[30] Now a third paper has appeared,[31] based upon material that shows the completed structures of the sac. Three species are included (*P. Artocarpus*, *P. odoratissimus*, and *P. coronatus*), so that the results may be regarded as fairly representative of the genus.

The primary sporogenous cell (overlaid by several layers of parietal cells) divides into a large inner cell and a smaller outer one, the latter dividing again. The embryo sac is developed by the innermost cell, which thus represents two megaspores. The usual divisions occur to the 4-nucleate stage (a pair of nuclei at each pole of the sac). The micropylar pair divides, and there is organized a normal egg apparatus and its attendant polar nucleus. Before this occurs, however, the two antipodal nuclei initiate a series of free nuclear divisions, accompanied later by wall-formation, until finally 64 or more antipodal cells may be formed before fertilization occurs. A variable number of antipodal nuclei are free and fuse with the micropylar polar nucleus to form a single large endosperm nucleus, or two such endosperm nuclei may be formed by the multiple fusions. In the formation of endosperm by the usual stages of free nuclear division, wall-formation, and centripetal growth, the author states that the "endosperm nuclei diminish in size as division proceeds, and this diminution in size is accompanied by a corresponding reduction in the number of chromosomes," although no count seems to have been made.

The excessive amount of antipodal tissue preceding fertilization certainly suggests that the antipodal cells are to be regarded as representing the vegetative tissue of the gametophyte, and so far as this feature is concerned, it seems safe to assume that it is primitive. In the organization of the egg-apparatus, however, it is not so much a question of the number of cells in the sac at the time of fertilization, as the number of divisions between the megaspore nucleus and the egg. In this case, since two megaspore nuclei are involved, there are just two successive divisions between a megaspore nucleus and the egg derived from it, instead of the usual three divisions.—J. M. C.

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[30] BOT. GAZ. **47**:485. 1909.

[31] CAMPBELL, D. H., The embryo sac of *Pandanus*. Ann. Botany **25**:773–789. *pls. 59, 60. figs. 2.* 1911.

Physiological behavior of Hypocrea rufa.—MEDISCH[32] has made a physiological study dealing mainly with the factors influencing the production of pigment by *Hypocrea rufa*, and the behavior of the fungus toward ammonium salts, nitrates, and nitrites as sources of nitrogen. The conidia of this fungus are green when grown on alkaline media, while in acid media yellow conidia are produced. When the fungus is grown in liquid media containing only glucose, the pigment diffuses into the medium, while the mycelium remains colorless. The medium passes through shades varying from green to yellow, orange, and brown. Certain salts, as the chlorides of magnesium, sodium, and potassium, potassium chlorate, and magnesium sulphate, have a specific stimulating effect on the production of pigment. This stimulation is limited for all these salts to isotonic solutions varying from 0.05 to 0.125 gram-molecules per liter. No pigment is produced in the presence of ammonium salts of strong acids, owing to the accumulation of free acid. The pigment production is regarded as an oxidation process, as it takes place only in the presence of oxygen, and the colored solution can be decolorized by reducing substances like sodium sulphite, hydrogen peroxid, and sodium hydrogen sulphide. The addition of an excess of calcium carbonate, infusorial earth, kaolin, and similar substances, decreases the intensity of color, probably as a result of absorption. The fungus grows with either ammonium salts, nitrates, or nitrites as a source of nitrogen. Nitrates are reduced to nitrites. With ammonium salts of strong acids, growth is soon depressed, and the formation of conidia is inhibited. As the fungus has no invertase, it cannot use cane sugar; however, in the presence of ammonium salts cane sugar serves as a source of carbon, owing to its inversion by the liberated acid. When nitrites are given as the source of nitrogen, conidia are produced only in the light, except when levulose is present. In that case, a few conidia are produced also in the dark. Ammonium salts are utilized in preference to nitrates, and ammonium salts of organic acids in preference to those of stronger mineral acids. Experiments to determine if the fungus assimilates free nitrogen did not give definite results. The paper contains a great number of data on the interaction of various substances in nutrient media in which fungi are growing.—H. HASSELBRING.

Peroxidase and respiratory chromogens.—A number of experiments to test the various methods of preparing peroxidase have been performed by PALLADINE and IRAKLIONOFF,[33] who find that the best method with tissues containing small quantities of proteins, as watermelon, pumpkin, etc., is to extract with water or 10 per cent NaCl, and precipitate the proteins with saturated aqueous $HgCl_2$. The enzyme is then precipitated from the purified filtrate with 95 per cent alcohol. The best solvent of the precipitated enzyme

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[32] MEDISCH, MARC, Beiträge zur Physiologie der *Hypocrea rufa* (Pers.). Jahrb. Wiss. Bot. **48**:591–631. 1910.

[33] PALLADINE, W., and IRAKLIONOFF, P., La peroxydase et les pigments respiratoires chez les plantes. Rev. Gén. Botanique **23**:225–247. 1911.

is K_2HPO_4. From their experiments they further conclude that peroxidase occurs in some plants as enzyme, in others as zymogen, and that the quantity present in different plants varies considerably. The smallest quantity in any of the plants studied was found in *Aspergillus niger* and the Saccharomycetes. A suggestion is made in this connection which is very important if true. They think it probable that yeasts are capable of producing alcoholic fermentation even in the presence of free oxygen because they contain very little or no oxidizing enzymes. The experimental evidence for this view is too slender as yet to be considered seriously; but if it proves to be true, it will clear up the relation of fermentation to the respiratory process.

The quantitative distribution of peroxidase and the respiratory chromogens shows a direct correlation, tissues rich in peroxidase containing much of the chromogens, and *vice versa*. Moreover, the tissues of plants are found to contain substances which are conceived to "stimulate" the color reactions used in detecting peroxidase. The products of alcoholic fermentation, which are rich in oxidizable substances, are placed among these stimulators of the formation of respiratory pigments. Finally, boiling of aqueous extracts containing chromogens is believed to render the formation of pigments impossible, either by changing profoundly the chemical nature of the chromogens, or by destroying the substances which stimulate the formation of the respiratory pigments which are produced by the action of such substances as emulsine and peroxidase on the chromogens. Most of the conclusions and suggestions seem to rest on a minimum of experimental evidence.—CHARLES A. SHULL.

The flora of Newfoundland.—The report of a botanical expedition to Newfoundland by FERNALD[34] includes the mention of many additions to the flora of the island, which is now known to possess 783 indigenous species. An inquiry into their geographical origin shows that about 60 per cent are boreal, including 28 per cent common to southern Labrador and eastern Canada. An additional 3.5 per cent are Canadian types not found in Labrador. A surprisingly large number of species are southwestern types found also in Nova Scotia, New Brunswick, and coastal New England, but unknown or rare in Quebec and Ontario. This class contains 274 species, or 35 per cent of the Newfoundland flora. At present 16 endemic plants are known, comprising 2 per cent of the flora.

To explain the abundance of plants identical with those of the Atlantic seaboard south of Newfoundland, the writer postulates the former existence of a bridge formed by an elevated coastal plain, composed of siliceous soils, connecting the island with Cape Breton and forming an ideal highway for the northeastward advance of plants which thrive on such soil. This siliceous bridge, according to the writer, would have been highly unattractive to such

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[34] FERNALD, M. L., A botanical expedition to Newfoundland and southern Labrador. Rhodora **13**:109–162. 1911.

species as *Adiantum pedatum*, *Thuja occidentalis*, *Lilium canadense*, *Calypso bulbosa*, *Lonicera canadensis*, *Solidago squarrosa*, *Aster macrophyllus*, and many other similar plants not found in Newfoundland, and which in eastern Canada "scrupulously avoid the more sterile areas." This explanation and the considerable lists of "calciphiles" indicate that the writer believes the vegetation to respond directly to the chemical character of the substratum.—GEO. D. FULLER.

Root tubercles of cycads.—Three papers on root tubercles of cycads, recording conflicting opinions, lay emphasis upon different features of these rather well known structures. ZACH[35] pays particular attention to the fungus hyphae, which branch profusely and become coiled together, after which the coils become digested. The fungus infests the tissues, causing the abnormal development, and the cell reacts by absorbing the fungus, a phenomenon which reminds the author of phagocytosis in animals. The relation is not symbiosis, but parasitism.

HOŘEJŠI[36] comes to the conclusion that the relation is symbiosis, and that the alga is the only cause of the abnormalities in the roots, the fungi and bacteria being merely the accompaniments of degeneration. The alga enters by the lenticels.

The third paper, by Miss SPRATT,[37] deals entirely with the life history of the alga, and gives a much more detailed account than has hitherto been available. She finds that the heterocysts are reproductive bodies, the contents of which break up into gonidia capable of reproducing the filament, as described by BRAND for *Nostoc*. The central body is described as a simple structure, incapable of anything but direct division. No reference is made to the work of OLIVE, whose technic and figures might have been helpful.

None of the three writers refer to the work of LIFE,[38] who described the mode of entrance of the alga and the general development of the root tubercle. —CHARLES J. CHAMBERLAIN.

Cretaceous flora of Japan.—SUZUKI[39] has described two conifers from the Upper Cretaceous of Japan as new. One of them is made the basis of a new genus (*Abiocaulis*), and is said to be nearest to *Abies* among living forms;

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[35] ZACH, FRANZ, Studie über Phagocytose in den Wurzelknöllchen der Cycadeen. Oesterr. Bot. Zeit. **60**:49–55. *pls. 2.* 1910.

[36] HOŘESJSI, J., Einiges über die symbiontische Alga in den Wurzeln von *Cycas revoluta*. Bull. Intern. Acad. Sci. Bohême **15**: 1–10. *figs. 24.* 1910.

[37] SPRATT, ETHEL ROSE, Some observations on the life history of *Anabaena Cycadeae*. Ann. Botany **25**:369–380. *pl. 32.* 1911.

[38] BOT. GAZ. **31**:265–271. 1901.

[39] SUZUKI, Y., On the structure and affinities of two new conifers and a new fungus from the Upper Cretaceous of Hokkaido (Yezo). Bot. Mag. Tokyo **24**:181–196. *pl. 7.* 1910.

the other is a new species of *Cryptomeriopsis*, the generic name suggesting the reputed affinity. A new fungus is also described, parasitic on the shoots of *Cryptomeriopsis*, and is referred to the Pyrenomycetes as a new genus (*Pleosporites*).

FUJII[40] has followed SUZUKI'S paper with a short discussion of the features of the cretaceous flora of Japan so far as uncovered, and especially contrasting it with the results of HOLLICK and JEFFREY in the United States. He announces a change of opinion as to the affinities of *Yezostrobus* and *Yezonia* (STOPES and FUJII 1910), being convinced now that this strobilus and stem, whether they belong together or not, are to be associated with the araucarians. The discussion of the causes of extinction is preliminary and suggestive rather then definite, attention being called to the influence of such factors as parasitic fungi, injurious gases from volcanoes, climatic changes, "inherent characters," etc. Even the cytological situation is included, the fluctuating numbers of chromosomes in angiosperms and their fixed number in gymnosperms suggesting a relation to the variability and hence adaptability of the former group, and the fixity and decadence of the latter group.—J. M. C.

An ecologist's garden.—A botanical garden of a new type, situated on Mount Aigoual, a peak of the Cevennes, and due largely to the foresight and energy of Professor FLAHAULT, has recently been described by SKENE.[41] The situation seems almost ideal for the study of many ecological problems, as it lies between the Atlantic and Mediterranean basins, with an elevation that permits the mesophytic vegetation of the former to thrive within a few miles of the xerophytic plants of the latter region. The presence and proximity of calcareous, siliceous, and granitic soils add to the value of the region for experimental purposes. In addition to the garden proper (800 feet below the summit), there is a plot at the very top of the mountain, and a bog which forms the source of a stream.

Since the founding of the garden (known as "L'Hort de Dieu") in 1903, a laboratory capable of sheltering a dozen people has been erected, and several thousand seedling trees and shrubs have been planted. Trees from all parts of the earth are being grown, in order to find those most suitable for forestry purposes in southern France, and to solve such ecological problems as the factors which limit tree species at certain altitudes. Not only the garden but the entire mountain is being made one gigantic ecological experimental plot.—GEO. D. FULLER.

Leaves of Calamites.—THOMAS[42] has undertaken an investigation of the leaves of certain species of *Calamites*, to obtain from their structure indications

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[40] FUJII, K., Some remarks on the cretaceous fossil flora and the causes of extinction. Bot. Mag. Tokyo **24**:197–220. 1910.

[41] SKENE, MACGREGOR, An ecologist's garden. New Phytol. **10**:64–68. 1911.

[42] THOMAS, H. HAMSHAW, On the leaves of *Calamites* (CALAMOCLADUS section). Phil. Trans. Roy. Soc. London B **202**:51–92. *pls. 3–5*. 1911.

of their environment. In short, it is a study of the ecological anatomy of fossil leaves. The leaves of *Calamites* are mostly known as impressions, and THOMAS has referred the structures he has been able to obtain to the better known impression forms. The petrified material used was obtained from the Lower Coal-measures (Halifax Hard Bed), and five types of leaf were distinguished. The twigs bearing the leaves proved to be quite interesting in stelar structure, especially in its relation to that of young stems of *Equisetum*.

The ecological conclusion is as follows: "The leafy twigs seem to have grown in a pendulous fashion, and the structure of the mesophyll and epidermis suggests that the habitat was a damp one. On the other hand, the leaves possess some xeromorphic features, such as the presence of fibers in the longer forms. The evidence points to a marsh or swamp forest as their habitat; this may have been near the sea, but if so the soil probably contained little salt."—J. M. C.

Transpiration in salt marsh plants.—Transpiration rates of cut shoots of *Salicornia annua* and *Suaeda maritima* have been found by DELF[43] to be equal to or greater than those from equal surface areas of such mesophtyes as *Vicia Faba*. The highest degree of succulence seemed to be accompanied by the highest transpiration rate per unit area. Relating transpiration to evaporation from a water surface, unit areas of *Salicornia* lost 32 per cent and of *Vicia* 26 per cent as much water as equal areas of water surface. It was shown that *Salicornia* is able to absorb water readily through the surface of its stems when submerged, and less convincingly that it does not absorb sufficiently through its root system to replace the loss by transpiration except in a humid atmosphere. This seems the more surprising, since TRANSEAU[44] has shown evaporation to be exceptionally high in salt marshes. The stomata in *Salicornia* and *Aster trifolium* appear to have distinct powers of movement in young plants early in the season, losing this plasticity at a later date.—GEO. D. FULLER.

Cytology of the ascus.—An account of the cytology of *Helvella crispa* Fries is given by Miss CARRUTHERS.[45] The cells of the hypothecium are one to several-nucleate, and some of the nuclei were observed to fuse in pairs, but no migration was observed like that in *Humaria*. An attempt was made to determine the number of chromosomes on the spindles in the vegetative hyphae. Apparently two chromosomes are present in the vegetative spindles, and four or eight on the spindles in the fertile hyphae, but owing to the minuteness of the objects not much importance can be attached to these observations. The

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[43] DELF, E. MARION, Transpiration and behavior of stomata in halophytes. Ann. Botany **25**:484–505. 1911.

[44] BOT. GAZ. **45**:217–231. 1908.

[45] CARRUTHERS, D., Contributions to the cytology of *Helvella crispa* Fries. Ann. Botany **25**:243–252. *pls. 2*. 1911.

divisions in the ascus follow the same routine as described by Miss FRASER in *Humaria rutilans*. The first mitosis is heterotypic, the second homotypic, and the third brachymeiotic, leading to a reduction without division in the last mitosis. The spores are formed by the astral rays in the manner described by HARPER for *Pyronema*.—H. HASSELBRING.

A parasitic orchid.—According to the investigation of KUSANO,[46] the vegetative body of the orchid *Castrodia elata* consists of a tuberous rhizome which multiplies through the production of tuberous offshoots. If these offshoots form no mycorhiza, they decrease in size and finally die without being able to flower, but if infected by the mycelium of *Armillaria mellea* they enlarge, flower, and produce daughter tubercles; it is therefore concluded that the orchid is completely parasitic upon the fungus. The mycorhiza is of the ectotropic type; occasionally, however, the fungus behaves as a parasite, penetrating deeply into the tissue of the tubers and causing their collapse in a manner similar to that seen in potato tubers attacked by the same organism.—GEO. D. FULLER.

Budding in Cycas.—While in Japan, Miss STOPES[47] noted the origin of the well known adventitious buds of *Cycas revoluta*. They arise on the upper portions of old leaf bases, some appearing more than 200 crowns back of the growing point. None were found arising from the axis, and the young buds do not seem to have any connection with the axis. The buds when removed grow into normal plants, but when they develop strongly upon the parent plant they give rise to the so-called "branching," and in such cases, of course, vascular connections are established with the main axis.—CHARLES J. CHAMBERLAIN.

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[46] KUSANO, S., Preliminary note on *Gastrodia elata* and its mycorhiza. Ann. Botany **25**:521–523. 1911.

[47] STOPES, MARIE C., Adventitious budding and branching in *Cycas revoluta*. New Phytol. **9**:234–241. *figs.* 7. 1910.

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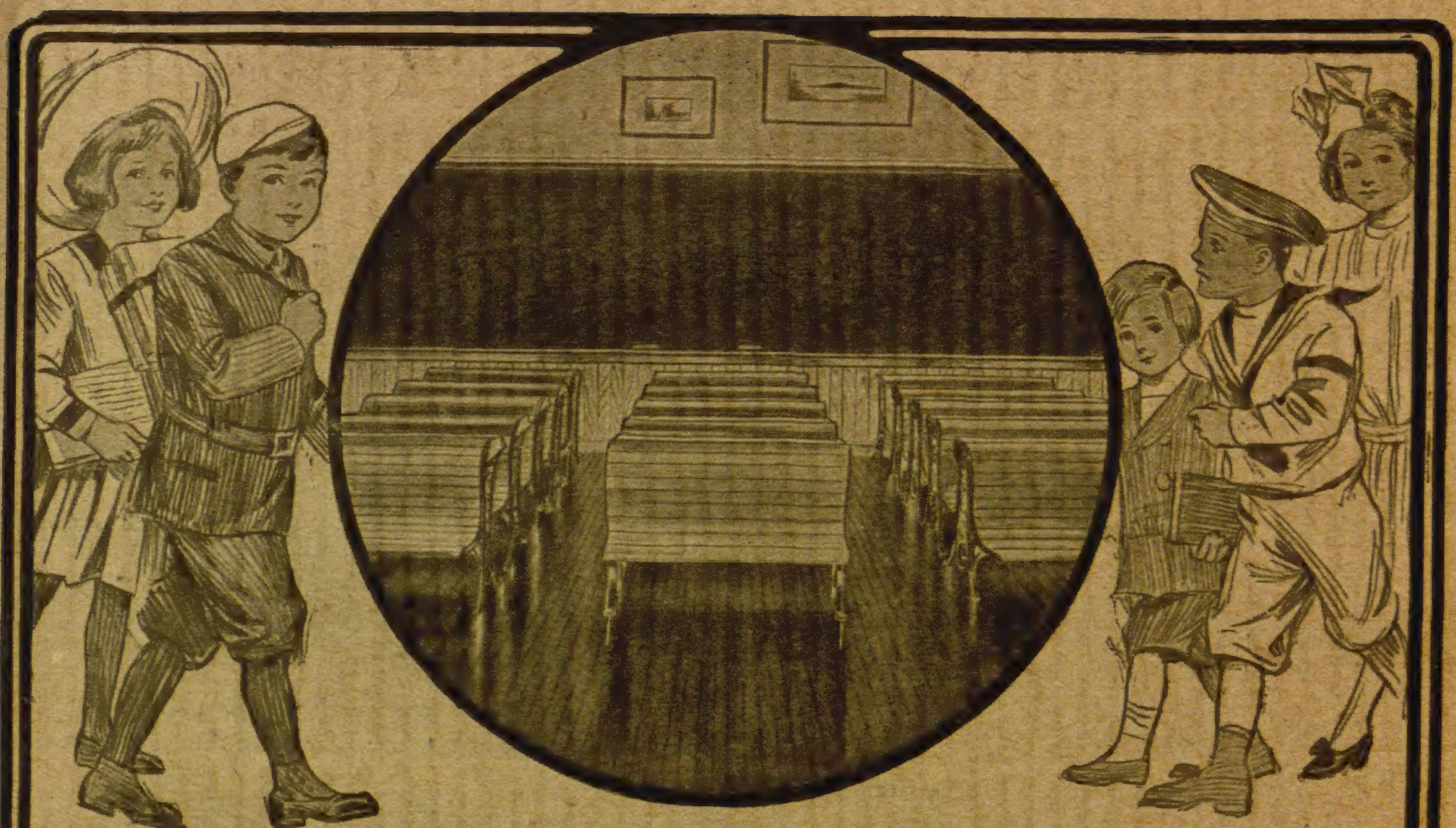

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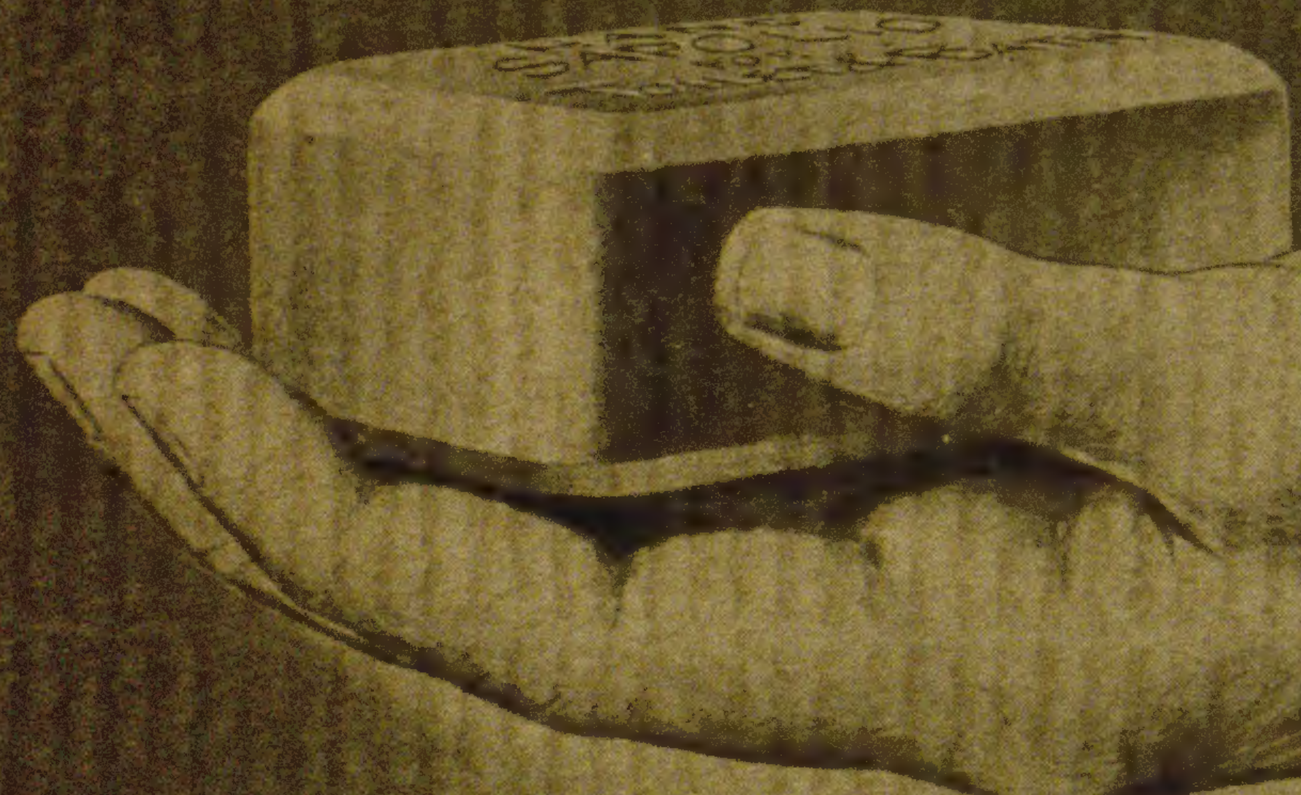

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